THE PHYLOGENY OF SEXUALITY AND TRIPHYLETIC EVOLUTION OF THE LANDPLANTS*

With 27 figures and tables

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Motto:
One must not fear hypotheses, if they are apt of making us able to look through a chaos of facts.

Oltmans

Introduction

All living beings in nature, plants and animals alike, are directed by two fundamental laws of nature, the instincts of self-preservation and of race-preservation. The instinct of self-preservation assures the vegetative life of the individual, while the instinct of race-preservation the survival of the race. This double process is realized in Unicellular organisms by the same individual while in Multicellulars vegetative life is assured by the so-called vegetative cells or organs, and the survival of the race by the sexual, reproductive cells or organs. A single cell or individual is sufficient to provide for vegetative life, whereas sexual propagation invariably requires the fusion of two contrasting, + and —, in the widest interpretation of a male and a female cell.

In the following we propose to investigate the patterns of the sexual reproduction in the vegetable kingdom, and particularly of the plants living in fresh water and on land. These patterns of sexual propagations have been realized in the development of the terrestrial flora during a period of two to four thousand million years, always by a necessary adaptation to environmental conditions of life. We do not propose to extend investigations to the history of developent of the sexual propagation of marine plants this time, because in our opinion the development of terrestrial and fresh water vegetation in the course of 2 to 4 thousand million years intervened independently of the development of see-weeds (GREGUSS, AXELROD). It should be noted, however, that the plants of the seas essentially and by necessity reached the same degree of development as did the phanerogams on land by our days. Here we want to point to the completely similar processes of the alternation of generations which intervened in the infinite course of times parallel to each other and in the same way both in the seas and in fresh waters and on land. (Sea-*Flagellatae,* fresh-water *Flagellatae; Cutleria-Musci; Dictyota-Pteridophyta; Laminaria-Gymnospermae* and *Angiospermae.)*

Similarly we do not dwell on the sexual propagations of *Fungi* and *Lichen* because they generally agree with the reproduction in the fresh-water *Algae;* moreover, the *Fungi*

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did not play a decisive role in the development of Cormophytes, at best they lived with them in symbiosis.

In the simplest unicellular fresh-water and land plants of course the sexual act could not have been in the past neither is it at present so complicated and of such high order as among the most developed plants, but the essence is the same both in the unicellular and in the highest terrestrial phanerogams.

To become acquainted with the thousand millions of years old history or philogeny of the sexual propagation of land plants, i. e. of the formation of the different developmental stages of sexuality, investigation must be started right at the beginning, where the first traces of sexuality can be conjectured, to gradually proceed towards ever more developed conditions. Where does the state appear for the first time, where does it begin, in which already the contrast of sexuality, its two forms, the male and female sexes can be suspected to exist?

Contrasts in nature

According to the ancient Greek philosophy, but also according to the philosophy of HEGEL, ENGELS and MARX, there is a constant contrast between objectives and phenomena of nature, and from this constant contrast evolution and progress are born. These contrasts are very frequent not only in inanimate nature but also in the life or organic world and one might even state that this is the general law. We may point in this respect to positive and negative magnetism in physics, to the so-called dipole-systems or to the + and — electricity where the two kinds of energy are of opposite nature, where the electric charges of the same kind repulse while those of different kind attract each other and when they merge, a third phenomenon, e. g. an electric discharge ensues. When, on the other hand, the two are present to an identical degree, there is apparent rest. The essence in both cases is that the same kind of energy has two essentially different features and both are characterized by the repulsion of the same kind and by the attraction of the different kinds or their readiness for fusion respectively.

In chemistry the same law of nature prevails. The compounds are generally acid or alkaline, possibly neutral. Acids and bases have contrasting features and therefore they eagerly unite, producing a new matter, (amphoter) a salt. In the salt there is something of both compounds, still it differs from both of uniting compounds (K_2SO_4). And if in the resulting salt one of the components somewhat prevails over the other then possibly an *acid salt* ($KHSO_4$) or an *alkaline salt* [Ca(OH)Cl] originates. We may also refer to the phenomenon of intersex or of the prevalence of male or female character in the organic world.

There are such contrasts, however, not only between the various compounds, but the same compound may have so called isomeric forms where there arise certain contrasts in the compounds in the mutual relationship of individual elements or groups of elements, in their special configuration; they may be possibly the reflections of each other and all these appear also in the character of the compound. One of the isomeric compounds e. g. turns the plane of the polar light to the right, the other to the left. Among the salts originating from the interaction of acids and bases the metal represents and carries of transfers the + electricity which for instance in electrolysis segregates at the — pole while the acid radical transfers the — electricity segregating at the + pole. Thus also in chemical processes the essential feature is that invariably contrasting forces act and a new compound different from the others is born from the interaction.

It is another well known fact e. g. that the relationship between cis and trans crocetin-dimethylester for instance in the male individuals of *Chlamydomonas eugametos* is 3 to 1 while in the female individuals 1 to 3 and a significant change of this relationship might change the character of the sexuality as well. From this on the other hand it may be inferred that in the living organisms there are similar or may be identical compounds as in the inanimate world so that there is no essential difference between the two spheres in this respect. In the living organisms and generally in the compounds of the living substance the same physical (electricity, magnetism) and chemical processes (replacement reactions) take place as in the inanimate (inorganic) substances. If it is so, however, the idea may be raised, and properly, that perhaps at the origin of organic world, when from the inorganic matters organic compounds and from the latter living substances developed, entirely similar and possibly even identical processes took place as those which we can observe in our in the inorganic and organic world.

Stage I. The origin of living substance

There can be and as a matter of fact is no doubt in our time that the development of the organic world started from the inorganic compounds. But as to how the first steps, the first attempts might have occurred, is widely open to discussion. We do not propose to deal with the various theories on this subject but accept as a postulate the statement that the living matter derives from the inert and his inorganic elements, and anyhow these first attempts took place, the fundamental principle i. e. the contrast between the elements and compounds existed already between the simplest elements and compounds. Electricity and magnetism were active in them from the very beginning and thus the possibility was given from the outset that more complex compounds could develop from the simplest ones, first simple and than more and more complicated organic compounds from the inorganic substances and finally from the inert and thus inorganic elements, and anyhow these first attempts could originate. According to the present state of science and also to individual opinions the most important constituents of this living matter could have been compounds of the nucleic acid type which are full of the most various dipole systems, to mention nothing else than the dipolic arrangement of the water molecules in them. The more complex a compound is, the more and the more various isomers it may possess, and might have possessed in the past, the fundamental principle, the chemical or electrical attraction and repulsion having remained in all of them. All this processes are likely to have taken place in a liquid and warm environment. From the increasingly more and more various isomers of the many kinds of compounds gradually organic matter complexes, so-called coacervates, and from these protoplasm type substances characteristic of the living matter separated, which as viewed at the light of modern science could be regarded already as the beginning of life. In this plasmatic matter gradually a nuclear substance started to form until finally the incredible variety of unicellular living beings developed upon the action of environmental factors. Since these primary cells had also been constituted by compounds and in the compounds, as an ancestral nature of law, the two contrasting effects, attraction and repulsion as well as the principle of fusion continued to exist, so already in the protoplasms separated into the most primitive cells the concequence of the positive and negative separation and fusion respectively existed, which ultimately may be considered already as the most rudimentary manifestation of the two sexes.

Stage II. Virophyta

It must be presumed that this sort of phenomena occur already in the viruses which are at the limit of life, since they also exhibit the + and − character. The *Virophyta* can not be qualified with certainty as living beings or inert matter. Science had established that they have some features suggestive partly of living organisms (propagation) while others point to inanimate matter (minerals). As to their propagation it only takes place in living cells or organisms, without showing, however, the least external mark of sexual reproduction. They show the first manifestation of sexuality in as much as contrasting com-

Stage II. VIROPHYTA

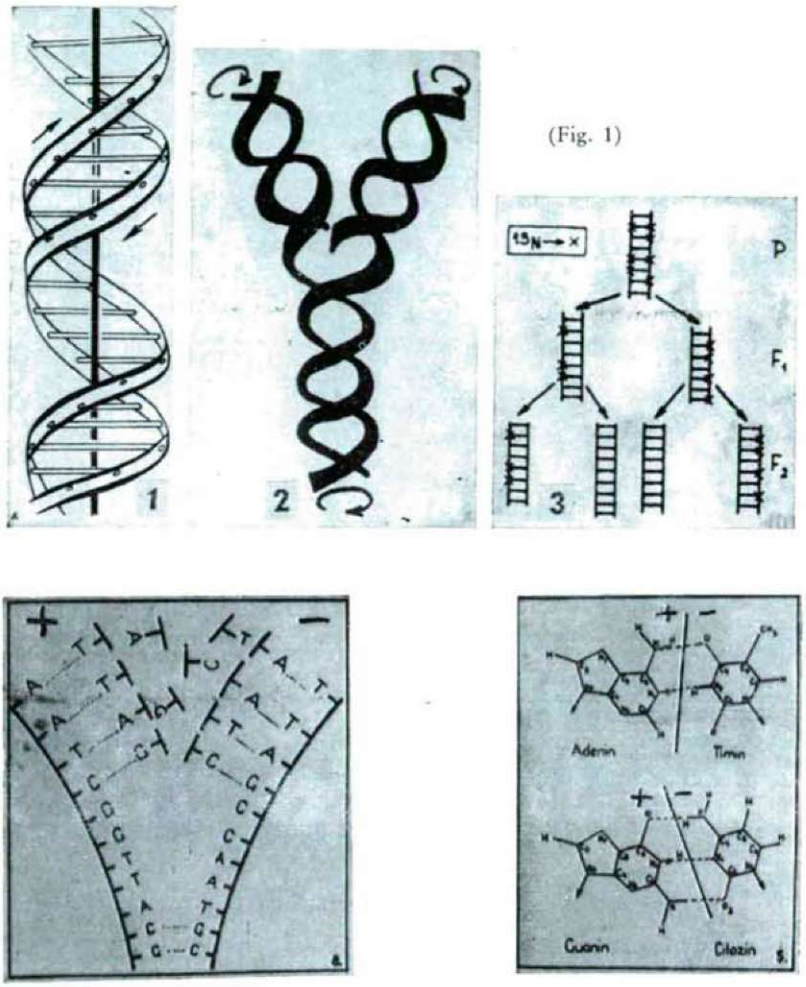


Fig. 1. Simplified WATSON—CRICK model on the structure of the DNA molecule. In the double spiral run the ribose and phosphoric acid radicals while along the perpendicular lines the purin and pyridin rings are arranged which are linked with two hydrogen bonds.

Fig. 2. Schematic illustration of the spiral self-reproduction of DNA.

Fig. 3. The DNA "increase" of the bacterium X marks the place of heavy nitrogens in the DNA of the "parent" (P) bacteria, while F_1 and F_2 designate the "labelling" of DNA originated in the first and second generations.

a) The two threads of the DNA separate and from the basic compounds the complementary thread develops.

b) Hydrogen bonds between the individual purin and pyramidin bases. (CSÁNYI, Természettudományi Közlöny 1962).

pounds, groups of compounds or their isomeric forms may exist in them, since for instance one strain of the same bacteriophage only attacks F—, while its other strain F+ individuals contrasting to the former. This contrast, according to most recent investigations, can be traced back to the chemical composition of DNA. It is known to-day beyond doubt that DNA is a large-molecule chain type matter that (except for some vira) transmits the hereditary informations from cell to cell and, in the course of the increase of the organisms, from parent to progeny. Some sections of the DNA chain can be already considered as essentially identical with the units of hereditary transmission, the genes. Thus the two spiral and scalar constructions of DNA (Fig. 1.) to all probability already represent the two opposite sexes, as evidenced at least by experiments with bacteria.

Such conditions might have prevailed in the history of the Earth about two to three thousand million years ago in the so-called azoic age.

Stage III. Anucleophyta

a) Bacteria

Evolution of the terrestrial life and the conquest of the continents essentially begins when the inorganic matter that became living assumes a cellular structure but no definite *nucleus* or chromosomes are developed in the cell as yet. The most characteristic representatives of this stage are *Bacteria* and blue algae *(Cyanophyta).*

The vegetative propagation of *Bacteria* occurs in the simplest way by simple division. When the individual divides in two parts, two individuals of the same kind develop from each half as that from which they themselves derive. This process then reiterates in an infinite number of cases, while the progeny remain both morphologically and physiologically equivalent to each other. The *Bacteria* do not possess a definite *nucleus* as yet, only a diffuse, protein type substance in which thymonucleic acid, DNS, is the most important compound and which to all probability has already a certain role in transmission by heredity. According to most recent investigations, in *Bacteria* already pairing occurs to a certain extent (Fig. 5.) which may be considered as a primitive manifestation of sexual propagation. But if there is sexual propagation, it can be traced back to the contrasting F+ and F— nature of the protoplasms or protein type compounds of the two merging cells and to the receding in distance of the two lines of the DNA spiral or their completion respectively (Fig. 4.). Thus among the *bacterium* individuals besides the chemical dimorphism some kind of sexual dimorphism, a physiological dimorphism takes shape, which appears more distinctly in the plants of cellular and nuclear structure.

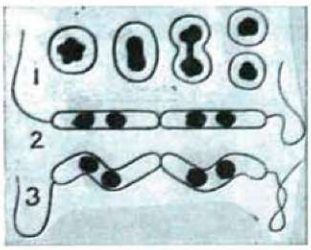
b) Cyanophyta

Essentially the same phenomenon is observed in Cyanophytes where in cell division central protein type particles and others suggestive of *nuclei* are forming. No perceptible sexual reproduction is known though in Cyanophytes; the separation of the *nucleus* type substance comes to pass in a very simple way, by

Stage III. ANUCLEOPHYTA

Fig. 5

Fig. 4



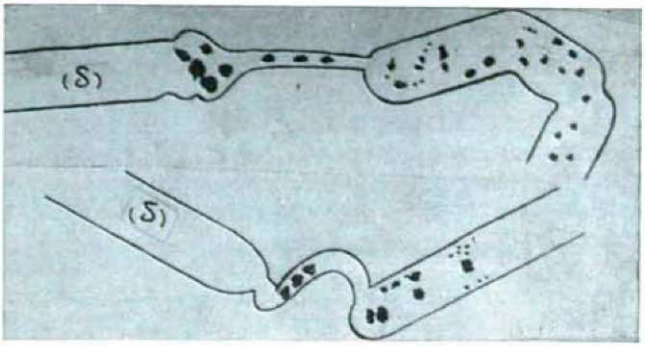


Fig. 6

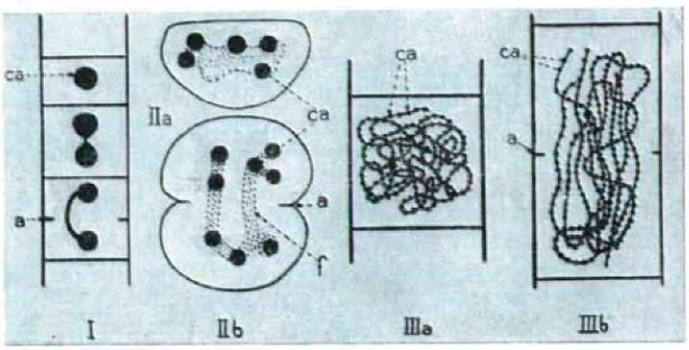


Fig. 4. The 3 types of *Bacteria*. In the cells black details mark the chromatinomous substance and its differentiation (According to CHADEFAUD).

Fig. 5. *Bacillus megatherium*. Between the two cells a conjugational canal forms. (According to CHADEFAUD, drawing after the photograph of LAMATER).

Fig. 6. *Cyanophyceae*. In the cells the chromatinomous substance (ca) is indicated by the details in black. I. *Oscillatoria terebriformis* (AG.) GOMONT. II. *Choococcus helveticus* NAEG. III. *Phormidium Retzii* (AG.) GOMONT; *ca* chromatinosomes; the place of cell division is *a* (According to CHADEFAUD).

division (Fig. 6). The so called sexual chromosomes representing the sexual character did not develop either, so that sexuality can be traced back at best, similarly to the phenomena observed in *Bacteria*, to the effect of the two lines of the DNA spiral. All parts of the cells developed in division are completely equivalent both from the morphological and physiological points of view. It is incompletely understood whether a sexual dimorphism exists or not among Cyanophyte individuals; but a chemical sexual dimorphism may be surmised on the analogy of *Bacteria* to all probability.

Such conditions might have prevailed in the azoic age of the Earth in the so-called Praecambrium, about 1000 million years ago.

Stage IV. Monadophyta

In the unicellulars with cell nucleus, the Monadophytes, a more developed state of sexuality appears more markedly and a further step can be noted as against the previous condition. All unicellular organisms may be generally designated as *Monadophyta,* irrespective of whether they belong to the various systematic groups such as *Flagellatae* or *Chlorophyceae.* Among the unicellular organisms besides the asexual, simple division, various degrees of the manifestation of sexuality can be observed which could have been developed only from the previous forms. These developmental stages are *isogamy, homogamy* and *anisogamy.* When Unicellulars are merging with each other, they can be already considered virtually as sexual cells, which are either *isogametes,* or *homogametes* or *anisogametes* (heterogametes). Those unicellular individuals which separate into both physiologically and morphologically equivalent gametes may be called *isogametangia,* as well, whereas those in which morphologically identical but physiologically different pairing cells arise, *homogametangia* and finally those in which morphologically different minor or major gametes develop, *anisogametangia.*

Isogametes

The isogametes are morphologically entirely, but physiologically only nearly identical. In these organisms the two kinds of sexual character is present to an equal extent; the chromosomes representing sexuality, to all probability did not develop yet; it seems that DNA, the compound determining the sexual character, did not separate yet in distinct chromosomes, but it is already present in the same *nucleus.* Whenever vegetative division of the individuals takes place in the two individuals that originated not only the particles of the protoplasm but also the compounds carrying sexuality, so the isomeric DNA too are equally localized. When, on the other hand, fusion takes place, amphoteric individuals both morphologically and physiologically, i. e. also as to compounds entirely equivalent arise at division. This is the same phenomenon as observed when from the interaction of acids and bases a neutral salt develops. Among the Flagellates this is a rather common phenomenon. E. g. the zygote of *Stephanosphaera pluviatilis* in condition of rest at the reduction — division within the hermaphrodite cell separates into gametes which are morphologically similar, but physiologically likely to be dissimilar and which unite still within the mother cell. Thus the individuals can be considered essentially as monoecious.

Homogametes

It marks a higher degree of evolution, when the individuals or gametes though externally equal and similar to each other, are physiologically already definitely different. In these organisms the DNA determining the sexual character in reduction division segregates in two contrasting isomers, as was seen in *Bacteria,* so that half of the gametes developed received DNA representing + character, while the other half got DNA of — character. Simultaneously also the so-called sexual chromosomes which are carrying them, have separated

(*haploid* section). These *haploid* individuals after vegetative division never unite with individuals carrying the same sexual character but only with the opposite ones. This is evidenced by the fact that if these individuals repeatedly form *gametangia,* the individuals (gametes) developing from these always become united with gametes arising from the different individuals, never with their „twins". The originating diploid *zygote* either continues to float (planozygote) or losing its cilia immediately retires to rest and transformed at the reduction division into *gametangium* separates in two male and two female individuals with physiologically different (positive and negative) chromosome sets *(Chlorogonium euchlorum, Ch. elongatum, Ch. neglectum, Gonium pectorale.* — Fig. 7). These two kinds of individuals (gametes) are morphologically entirely identical and differ only physiologically, so they are dioecious. The physiological difference to all probability must be traced back again to the influence of DNA, possibly upon the effect of the more intensive light. Thus these gametes substantially differ from the *isogametes* and therefore may be regarded as *homogametes,* whereas the individuals engendering them, as *homogametangia* at the time when they do engender them. The homogametes or *homogametangia* respectively represent the second developmental degree as against the isogametes or *isogametangia,* i. e. the dioecious form against the monoecious. Several examples of this are known also from the Flagellates.

Anisogamy

Evolution made a further step by the realization of *anisogamy.* In this developmental stago the gametes not only physiologically but also morphologically differ from each other, i. e. sexual dimorphism subsequently to the dimorphism of chromosomes has spread to the morphology of individuals, essentially also to the form of the gametes, so that *gamete dimorphism* ensued (Fig. 7). A number of classic examples are known for this particularly in *Chlamydomonas* and *Chlorogonium (Chlamydomonas fonticola, Eudorina elegans)* and in some cases evolution goes so far that the cell content of the one individual actually develops into a true immobile ovule *(oogonium)* in *Chlorogonium oogamum* while the other cell disintegrates into an infinite number of biciliate, so-called microgametes (Fig. 7). Consequently, already here the stage of historical evolution occurred in which the female gamete has finally lost its mobility, became immobile and maintained this condition of immobility during the history of evolution even in the most developed terrestrial phanerogams. The male gametes, however, retained mobility with the aid of their cilia as long as fresh water has been the medium between the two kinds of sex and had lost this capicity only when in the gymnospermous and angiospermous condition wind and insects took over the mediatory role.

The essential in the Unicellulars is, consequently, that the individuals are either monoecious and, when pairing *isogametes,* or dioectious and when they unite either *homogametes* or *anisogametes.* The establishment of these three developmental stages as soon as in the unicellular condition is the more important because it repeatedly occurs according to the same pattern in the history of evolution of the vegetable kingdom. It had to repeat itself by necessity, because it is the fundamental law in the history of evolution of sexuality.

Evolution makes a further step e. g. in the case of *Eudorina,* when separate male colonies develop, breeding spermatozoids, while in another colony only

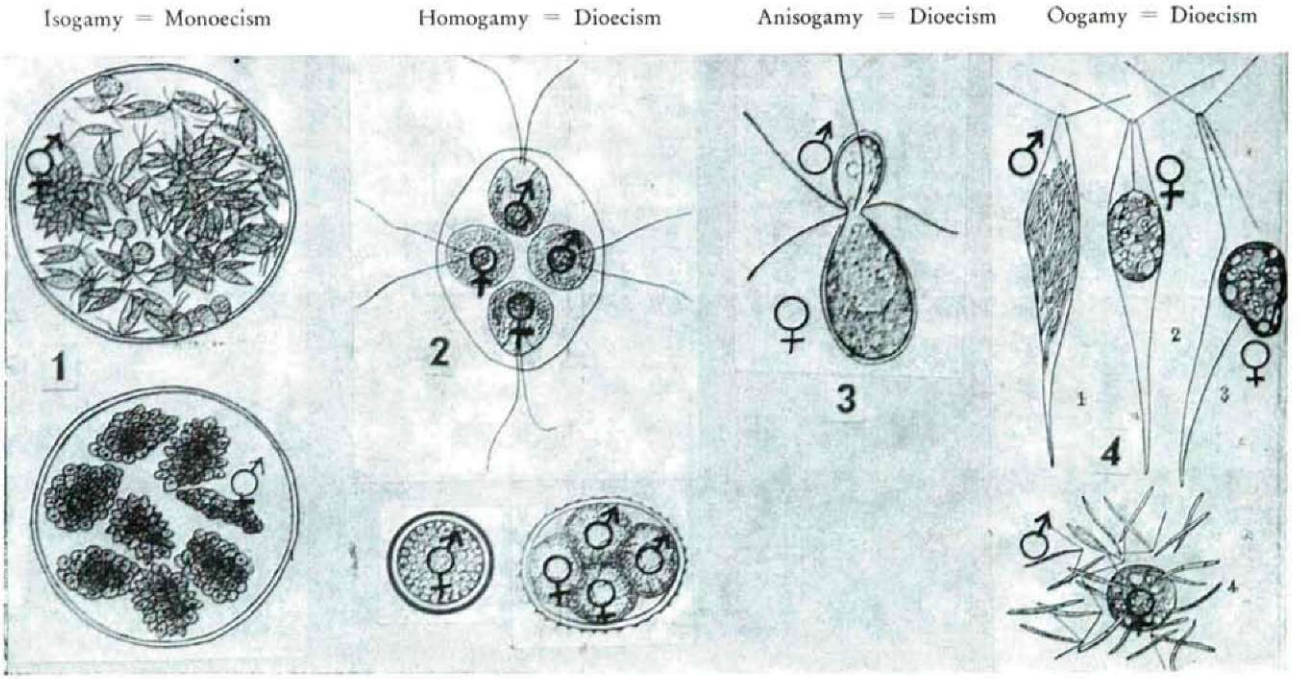


Fig. 7. *Isogamy* of *Stephanosphaera pluviatilis* within the cell wall. II. *Homogamy*. 2 male and 2 female type homogametes of *Gonium pectorale* within the cell. From the zygospore by reduction-division 4 gametes arise from which 2 are of male, 2 of female type; they are morphologically equal and differ only physiologically, so they are homogametes. III. *Anisogamy*. *Chlamydomonas fonticola*. The smaller is the microgamete, the larger the femaletype macrogamete. IV. *Oogamy*. *Chlorogonium oogamum*. 1. In the male-type individuum a great amount of spermatozoids, 2. in the female-type individuum a single immobile egg, 3. egg emerging from the cell, 4. the egg is surrounded by many spermatozoids.

individuals, gametes of female character develop. The spermatozoids released from the male *gametangia* surround the female colonies, uniting with and fertilizing them (primitive allogamy). The result of the fertilization consists in several unicellular zygotes which secrete a thick wall around themselves to start, after a certain period of rest, reduction-devision. From the 2 male and 2 female individuals (tetrades) originating thus only one develops further while the three other brothers degenerate. Accordingly, the remaining fourth individual can be either of male or of female character. In the final result half of the zygotes developed from the female colonies, assumes a male the other half female character. Hereby the sexual dimorphism advanced again by a step because physiological dimorphism appears now not only among the colonies, i. e. cell groups but also between zygotes.

Essentially the same process occurs in the dioecious *Volvox dioicus*. Also in the *Volvox* monoecious and dioecious colonies occur *(Volvox globator)* among whose vegetative cells *antheridia* of male character and *oogonia* of female character appear. The spermatozoids ripen earlier than the eggs and only exceptionally fertilize their own egg, when autogamy ensues (though allogamy is more general). In the dioecious forms reduction-division of the zygote occurs whereas the zygote of the monoecious forms after the first heterotypical cell division immediately develops into monoecious colony.

In Flagellates — as shown above — the condition of *Volvox* and *Eudorina* is most developed where sexual differentiation is realized not only between the individual gametes but also between colonies. Spherical cell association trend seems to have reached herewith its highest degree; it actually did not develop further, the developmental trend simply came to an impasse.

Besides the spherical cell association form nature tried out also another potentiality, when the cells after their divisions rallied not in spherical colonies but in cell-filaments and lamellae. Evidently this direction was more suited for evolution because starting from the unicellular organisms a further evolution ensued, and first the cell filament than the cell lamellar and cell corpuscular *Algae* developed (Fig. 8).

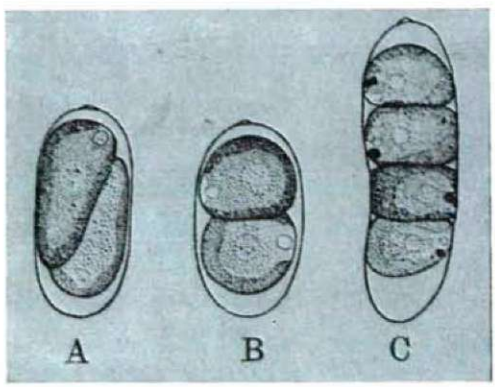


Fig. 8. *Chlamydomonas seriata*. The zygote first divides with an oblique wal in two parts. *A)* the oblique wall subsequently assumes a horizontal position *B)* then it repeatedly divides with a horizontal wall and hereby a short cell-row originates. *C)* The simplest pattern of cell filament formation. According to. PASCHER.

The problem of sexuality

In connection with the phenomena observed so far the question arises, why do gametes of different sex, organs of reproduction or individuals of different sex develop in nature, one of which exhibits male (+) the other female (—) character and generally what is the reason why invariably gametes and reproductive organs of two opposite sexes arise which phenomenon is manifest not only in the simplest living beings in the *Bacteria* and in the most developed plants but in all living organisms. This question, the problem of the transmission of sexuality by heredity materializes in the strict regularity of the sexual propagation of living beings. Why is it that in nature once male, then again female individuals or two kinds of mating cells originate and that only these unite with each other?

Already MENDEL observed that sexuality is an inherent property of living beeings, exactly as e. g. size, colour or shape of peas. Recent research work revealed that besides the determining role of DNA, properties connected with sexuality are always linked in the *nuclei* with one or two chromosomes of definite size — the shape and size of which, however, is different from the others — the so-called *sexual chromosomes* or *heterochromosomes*, and that the sexual properties of the individuals are always transmitted to the progeny through the instrument of these, as if all properties related to the sexual character were localized in these special chromosomes. In all plants and animals which are heterogamous and even in man, when the sexual cells develop, in the *nuclei* besides the other vegetative chromosomes (autosomes) one or two so-called sexual chromosomes (x or y) are formed (Fig. 9). These sexual chromosomes are responsible for it, among others, that now male now female individuals develop and that certain properties are linked to one sex or the other. Why is it important to

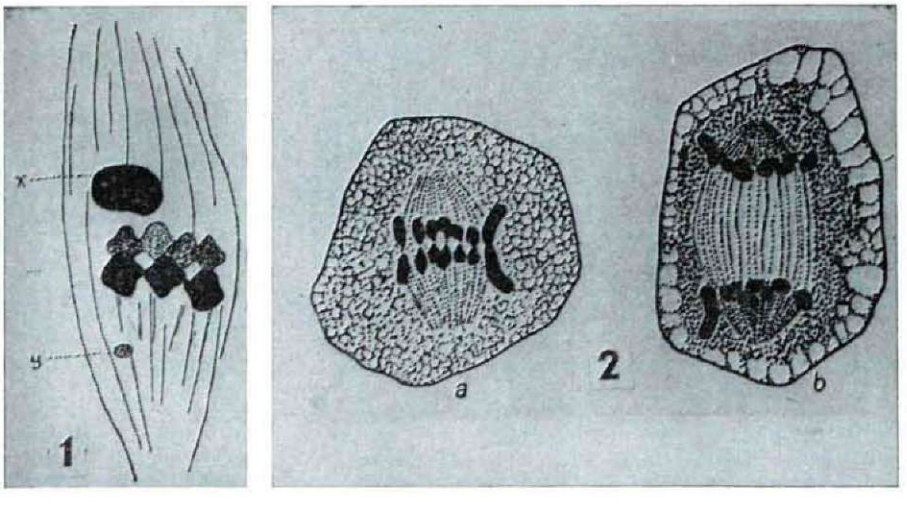


Fig. 9. *Spherocarpus terrestris (Musci).* In the metaphase of reduction-division X and Y chromosomes. First division of the pollen mother cell of *Melandrium album* (reduction-division) *a)* early, *b)* late anaphase, with separation of the X and Y chromosomes (according to HARTMANN).

stress this regularity in the evolution of the vegetable kingdom from the very beginning, in the discussion of the simplest plants? Because in most of the living beings invariably such individuals or organs of propagation develop in which the sexual character always manifests itself in the appearance of the reproductive organs and in the finer structure of the gametes developing in them.

The simple explanation of this phenomenon materializes in the fact that in the *nuclei* of the sexual cells of all heterogamous individuals at the origin of the sexual cells always a certain number of *n* chromosomes appear from which one is invariably the socalled *sexual chromosome* (x), while in the vegetative cells, the so called autosomes, the double number originates (nn + xx). This sexual chromosome has a different shape and size both in the male and female gametes. For instance in the vegetative cells of the female individuals (FF) there are a certain amount (2n) of chromosomes and two identical,' so called homologous sexual cromosomes (xx) (Figs. 10., 11). As a contrast, the male individual also

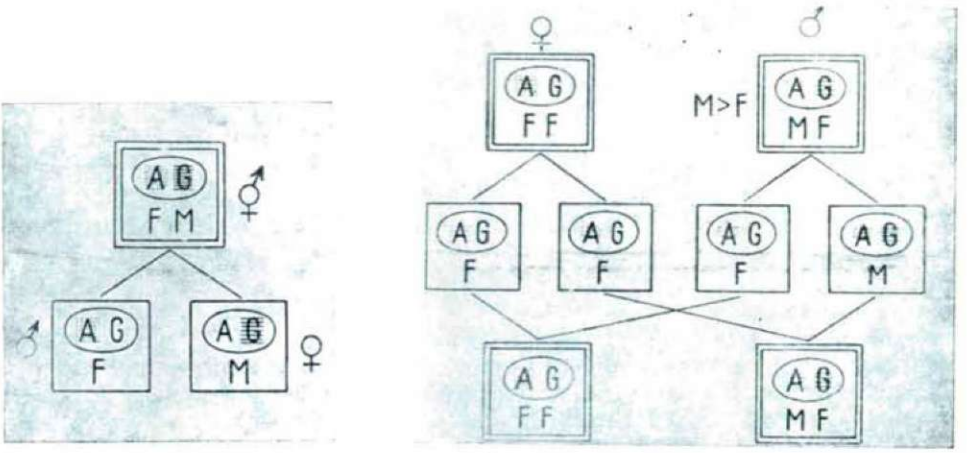


Fig. 10. The scheme of the haplogenetic sexual determination e. g. in a dioecious moss. A and G mark the male and female potentials. F is the realizator directing the female trend and thus limiting the development of the male trend. M is the realizator of the male trend. In diplophase (in the sporophyte above) F and M are also present. M is the male realizator which prevents the female G potential from developing; therefore G is cancelled (similarly the female realizator F inhibits the male potential, therefore A is cancelled with dotted lines). In reduction-division one gone contains only F the other only M, whereas both contain A and G. Consequently in the one case (left) F inhibits only A and as a result the gones or spores and the gametophyte derived from them will be female. In the gone which contains M, only G will be inhibited, consequently the result will be male. (According to GUTENBERG).

Fig. 11. Diplogenetical sex determination in Phanerogams, according to the *Bryonia* experiments of CORRENS. In all individuals male and female potentials (A and G) are localized. All female individuals contain in a homologous pair of chromosomes a female realizator F so they are homogametes of female trend. As a contrast the males contain two different realizators, namely a female determinator F, and a male determinator M, so the males are heterogametic (first row of the sketches). Consequently in reduction-division in all pollen mother cells two of the four pollens are of the F and two of the M type (2. row). At the fusion of the sperms with the egg when those containing F realizators are fertilized, from the fusion of F with + F a female plant arises. If on the other hand M merges with F, a male individual originates, since the trend inherent in F is stronger than in M. Lower row of the sketch (According to HARTMANN).

contains 2n autosomes and besides x or x and y sexual chromosomes (MF). Accordingly in reduction-division most female individuals produce only one kind of sexual cells, i. e. gametes of female character (n+x) (F); this is why the female individuals are generally *homozygous* (FF). Most male individuals on the other hand are heterogametic (F and M) because they produce two kinds of sexual cells namely n+x and n+y or only n gametes. If e. g. the homozygous egg (F) (n+x) is fertilized by a male sexual cell of a similar chromosome set (F) (n+x) female individuals (FF) (nn+xx) would originate whereas if the homozygous egg (F) (n+x) is fertilized by a different heterogametic sexual cell (M) (n+y), male individuals (MF) (nn+xy) would originate. Thus sexuality is determined in the first place by the sexual chromosomes and by DNA activity localized in them. And since in reduction-division gametes determining the two kinds of sexes originate to an equal ratio (50 : 50 per cent), this is the explanation of the fact that in the vegetable but also in the animal kingdom the two sexes are represented more or less at an equal rate. This regularity which is based on strict cytological foundations had an important part in the course of the evolution of plants; it is a phenomenon accompanying evolution from the unicellular organisms to the most developed forms of the vegetable kingdom, the *Angiospermae* of the Phanerogams. Such aspects should determine our view of the phenomena related to sexuality among the unicellular organisms. Although nature had accomplished a wide range of variability among the unicellular organisms as to the aspects and transmission by heredity of sexuality, still in the final result all this must be traced back to the three ancestral types i. e. isogamy (monoecism), homogamy (dioecism) and anisogamy, which conditions have been directed always and everywhere by the forms of opposite effect of the various compounds, and DNA in the first place. The monadophyte condition in the history of the Earth attained its highest degree in the *Praecambrium* and *Cambrium* when the four developmental stages referred to above had realized in incredibly manifold forms which is verified also by the infinitely varied forms of the recent freshwater and sea Unicellulars.

Stage V. Algophyta

Multicellular state.

After this short digression let us revert to the unicellular organisms. The plant kingdom did not remain in this simplest unicellular state. The next step in evolution during a „try-out" of many million years was the *association of cells,* when the dividing cells after having originated did not completely separate from each other but remained in further contact and connection in colonies, cell-families, beside oneanother. This juxtaposition has been realized in the form of *cell filaments, cell-lamellae* (cell bodies) or *spheres.* In all three directions the division of sexuality again continued in the ancient three types of *isogamy* (monoecism), *homogamy* (dioecism) and *anisogamy* (oogamy). *Volvocales* exhibit the spherical degress of evolution *(Pandorina, Eudorina, Volvox)* while the possible evolutionary degrees of the cell filament and lamella state materialized within the *Chlorophyceae* (in the *Ulotrichales, Siphonales* types) with a great variety. It seems, however, that the sphorical trend was not a form suited for further evolution and reached its peak in *Volvocales;* instead or

besides the filamentons, laminar and cell body trends developed further because they were adapted to the conquest of fresh waters and of the continents.

Branching forms.

There is no doubt, neither can be, that the unicellular plants derived from the multicellular and, as referred to above, initially from the spherical or filiform types respectively. The filiform type might have originated from the exceedingly varied unicellular organisms by repeated branching (*Vaucheria*, Fig. 12); or else the cells originating as a consequence of the one-way division

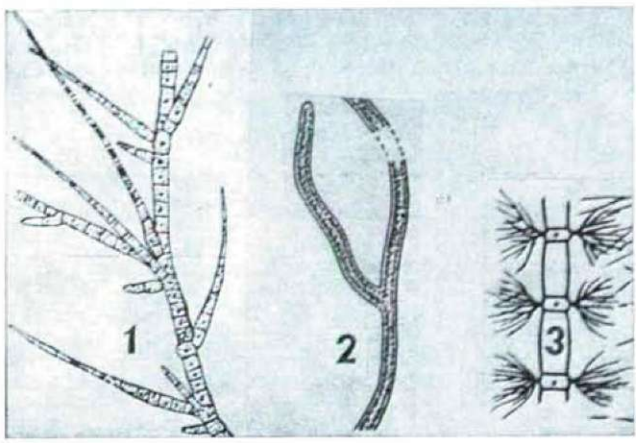


Fig. 12. Three types of branching in *Chlorophyceae*. 1. *Stigeoclonium subuligerum:* monopodial. 2. *Vaucheria sessilis:* dichotomous. 3. The whorled branching in *Drapalnaldiopsis indica*. The stages of development are identical, still there are three types of branching. (According to PASCHER and CHADEFAUD).

formed cell filaments *(Cladophora, Ulotrix Drapalnaldiopsis)* thus giving rise to organisms of primitive structure branching in different ways. Any kind of branching consists in an increase of surface which is favourable for the vegetative life of the plant; at the same time a possibility arises for cells and organs to come into being which would assure the production of progeny.

It should be noted here that the various forms of branching started right from the unicellular plants and this trend as a basic principle remained up to the most developed plants. Since in our view, branching has a decisive role in the history of evolution of the vegetable kingdom, this problem must be briefly dealt with in order to facilitate understanding of what follows.

When the cells divide in one direction of space with transversal walls or possibly with apical cells, actually non branching cell filaments originate. Several such forms are known among green algae (*Spirogyra, Zygnema, Ulotrix* etc.). Branching occurs when the cells or cell-groups formed increase in two or three directions of the space and in the meantime assume various forms.

Some unicellular *Vaucheria* e. g. are branching repeatedly and dichotomically. This is the *dichotomical* branching. In the filamentous algae *Cladophora, Bulbochaete* at the meeting of the terminal cell-walls lateral filaments originate which, however, are always younger and less developed than the main branch

from the side of which they came into being. Thus here a central *axis (monopodium)* exists from the side of which the lateral branches originate. This is the *monopodial* branching (Fig. 12).

The filamentous *Drapalnaldia* or the recently discovered *Drapalnaldiopsis indica* also have a central filament axis which, however, consists of regularly short so-called nodial and much longer internodial cells. From the short nodial cells, i. e., from the same height, several secondary but equivalent lateral filaments originate. Consequently this branching essentially differs from the first two, from the monopodial and dichotomous. This ancient primitive form of branching is termed as *whorled* or *verticillate*. Comparison of the three forms of branching reveals that all three are characteristic to such a high degree according to the author on this degree, that none can be derived from the other. The attempt to derive monopodial branching directly from dichotomical branching by an overgrowth of branch is not valid and lacks all positive evidence. Similarly the verticillate branching can not be derived either from the monopodial or from the dichotomical. All three kinds of branching are ancestral types the simplest form of which can be found even in our days among the fresh water algae of filamentous structure. This phenomenon also proves that the evolution could have started from the unicellular condition towards the filamentous stage in the fresh water at the very beginning in several directions, i. e. the trend of evolution within the green algae could have been polyphyletic right from the beginning.

To this finding it should be immediately added that the same types of branching are realized in sea weeds which supports the assumption that the further development of the branches of fresh water algae could have occurred independently of the development of sea weeds. Among sea weeds too these three types of branching have materialized because only these three main types are possible. But to whatever branching type the fresh water Algae may belong, they agree in that the gametes assuring sexual reproduction form on the same individual, when they are monoecious, or on two similar individuals, when they are dioecious, or on two individuals of different form (anisogamy). All three developmental stages within the Algae are actually replicates of those fundamental states which were observed in unicellular organisms except for the sexual acts having been already transferred from the single cells — as a consequence of division of functions among the cells — to more developed states assuring better possibilities for further evolution, namely to the cell filaments or lamellae, cell bodies respectively.

In the monoecious, multicellular, filmentous individuals the haploid gametes of the same size and of opposite chemical character merge in the water into an unicellular diploid zygote which unicellular zygote after a shorter or longer state of rest undergoes a single reduction division and the haploid cells formed grow into haploid cell filaments. The sporophyte — i. e. the diploid generation — is in this case only unicellular (1) as against the gametophyte that possibly consists of an infinite number of cells (∞). Thus from the zygote only one kind of filoments develop which are of hermaphrodite character. This is observed e. g. in the monoecious green alga *Acrohaete repens* or in the monoecious *Oedogonia* or in the monoecious *Bulbochaete* (Fig. 13).

In the dioecious filamentous algae the position is essentially the same, with the difference that here male and female gametes are produced by different

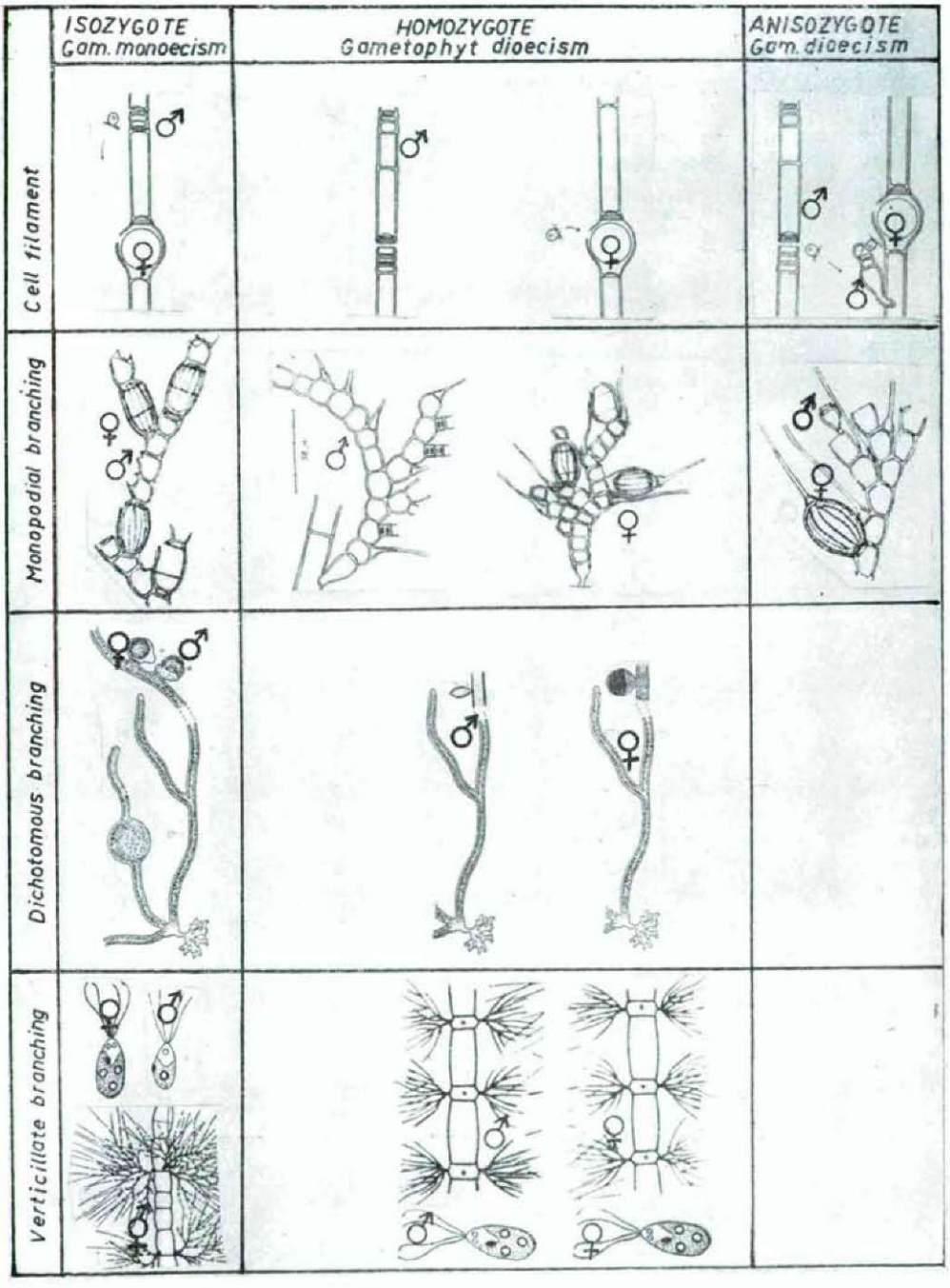
filaments. Both filaments and gametes are morphologically similar to each other and exhibit only physiological differences. From the fusion of morphologically similar but physiologically different haploid gametes in this case too only a unicellular diploid zygote arises which for a shorter or longer period goes to rest to give rise subsequently after reduction division to half male half female type but morphologically similar filamentous individuals from the haploid cells. These zygotes are morphologically completely identical (isozygotic) and differ only cytologically, namely in the different chromosome structure from the isozygotes. Therefore they are called, to distinghish them, on the analogy of the term homogamete: homozygotes.

This stage of development is realized particularly in the dioecious *Bulbochaete, Oedogonium, Vaucheria,* in the dioecious, *Drapalnaldia.* The + and — character is induced also in these cases, to all probability, by the compounds determining sexuality, mainly by DNA, within the *nucleus;* these compounds are arranged and localized respectively in the so called sexual chromosomes that determine sexuality.

Even this stage of development shows a further advance when sexual dimorphism extends to the gametophytic individuals originating the gametes and when this step is made, the multicellular filamentous gametophytic individual has not a single cell left without sexual differentiation. Thus the sexual differentiation of the gametophyton is completely realized in this state but at the same time the unicellular diploid zygote which alone represents the sporophytic phase, morphologically still completely agrees with the equally unicellular iso- and homozygote. So there is no morphological difference among

Fig. 13. *Monoecism, homomorphous dioecism* and *heteromorphous dioecism* in Chlorophyceae. *Upper row.* 1. On the same individuum of the monoecious *Oedogonium nobile* WITTR. the polyciliate male spermatozoids and the egg (monoecism) develop. 2. Homomorphous dioecism in *Oedogonium capillare* (L.) KÜTZ. In the one male individual the polyciliate spermatozoids while on the others which are similar to the male individual, only the eggs (oogonia) develop. 3. Heteromorphous dioecism in *Oedogonium diplandrum* JUR. In the one male individual androspores arise from which a few cells high dwarf males originate; these settle in the vicinity of the female *oogonium* and their gametes fertilize the egg (oogonium).
2. row. Monopodially branching cell filaments. 1. Monoecious *Bulbochaete.* Some cells of the cell filament develop into *oogonia* while others to *antheridia.* Thus the individual is monoecious. 2. A male plant of *Bulbochaete annularis* and a fernale plant. Dioecious macrandrous species. From the two kinds of individuals of *Bulbochaete* sp. the one forms androgametes which settle on the female individuals near the *oogonia* that develop on them. Between the two sexes there is sexual dimorphism, heteromorphous dioecism. 3. Thus the individual is dioecious. The same is found in a third species where the oogonium and the antheridium of dwarf male character (♂) develop on two kinds of individuals and came subsequently into the female individual so that between them heteromorphous dioecism exists.
3. row. On the same individual of the dichotomously branching filamentous alga *(Vaucheria sessilis)* are found the *antheridia* and the *archegonia,* consequently the individual is monoecious. On one individual of *Vaucheria dichotoma* archegonia only, while on the other antheridia only develop, consequently the individuals are dioecious.
4. row. From the individual cells of the filament of verticillate branching smaller microgametes and larger macrogametes of male character develop. Thus the individual is monoecious. In the cells of some individuals of *Drapalnaldiopsis indica* swarming spores with 4 cilia of only male character and in the cells of other similar individuals 4 ciliate swarming spores of female character originate. Thus the species is dioecious. This means that also within the *Chlorophyceae* the same developmental phases occur but with essentially different branchings.

Stage V. ALGOPHYTA



the three types of zygote. Since, however, from the one (isozygote) after reduction division monoecious gametophytic filaments (first vertical row), from the other zygote gametophytic filaments of two sexes i. e. dioecious individuals (homozygote, middle longitudinal row), while from the third equally dioecious individuals of different shape arise (third vertical row), so to distinguish this third developmental stage from the homozygote we call it anisozygotic.

According to what has been said above, also in the filamentous Algae as to the distribution of sexuality three developmental stages can be distinguished, similarly to the unicellular organisms, namely the monoecious isozygote, the dioecious homozygote and the dioecious anisoxygote of different shape. All three represent the unicellular sporophytic stage as against the unicellular sporophyton.

Since we have distinguished these three developmental stages, let us now examine which way these main types materialized within the phylum Algae.

The monoecious isozygotic developmental stage occurs within the *Chlorophyceae* e. g. in the *Capitularia* with monopodial branching, e. g. in *Vaucheria dichotoma* or *Dichotomus* or *Phycopeltis* pertaining to the dichotomically branching *Siphonales* or in the *Drapalnaldia* forms of verticillate branching. In all three the developmental stage is the same, monoecism, still the branching is strictly of three or four different types. The assumption seems justified that these types have reached the same developmental stage, monoecism, independently from each other, thus to get so far they had set off, starting from the Unicellulars, probably from three directions (monopodial, dichotomous and verticillate).

Exactly the same applies to the homozygote. Most of the *Vaucheria* are dioecious. Similarly, from the *Drapalnaldiopsis* with verticillate branching rather many are dioecious, but also in *Ulotrices*, *Oedogonia* and *Bulbochaete* dioecious forms are known. Consequently the filamentous algae have reached also the dioecious stage from three or four directions.

A still more developed state materialized in the dioecious *Oedogonium* and *Bulbochaele* by the development of dwarf males where two gametophytes of different shape and size come into being. The zygote, however, is again unicellular, giving rise by reduction division to gametophytes of two different sizes and forms, thus it is *anisozygotic*. According to these facts, sexual dimorphism materialized in a striking manner among the gametophyton individuals, while the zygote remained unicellular.

Homomorphous alternation of the two generations.

Within the Algae development made a further advance, since in some cases so called homomorphous individuals arise, i. e. both gametophytes and sporophytes are quite similar to each other. The sporophytic individuals of the morphologically entirely similar *Cladophora* are completely analogous as to their morphological aspect, but physiologically they give rise to two types, + and — of four ciliate so called zoospores from which again morphologically identical dioecious, i. e. + and — gametophytes originate. One of these forms positive (male)-type while the other negative (female)-type two-ciliate gametes. The haploid gametes at first unite to form diploid zygotes; these, however, do not remain in a state of rest, but develop into diploid individuals quite similar

to the haploids and as such give rise in some of their cells by reduction division to two types of (+ and —) four-ciliate zoospores. Exactly the same homomorphous developmental stages materialized in the recently discovered *Drapalnaldiopsis indica,* with the essential difference, however, that *Cladophora* is a filamentous green alga with monopodial, while *Drapalnaldiopsis* with strictly verticillate branching. Thus again the same developmental stage and identical alternation of generations are found, but in the one case it is a filamentous green alga with monopodial, while in the other with verticillate branching. The two algae arrived from different directions at the same developmental stage. Probably also in *Hepaticae* such phenomenon occurs, although it had not been observed yet so far. In the above developental courses most probably already such a phase can be seen. (Fig. 14). Thus here already a phase appears that will repeat itself essentially in the evolutionary history of the terrestrial plants, marking somehow the further path of evolution. These are the so-called homomorphous individuals. Most probably this phenomenon materialized also in the *Psilophyta* of the Devonian (see later).

The further march of evolution is indicated within the *Chlorophyceae* by the *Coleochaete* species which are monoecious, thus developing one type of individuals which give rise to *antheridia* from which male gametes arise and to *oogonia.* The zygote formed from the fusion of haploid gametes secretes a thick wall, subsequently remains for a certain time period in state of rest and then first produces a reduction division within the thick wall, to divide later into 8 to 16 cells *(C. scutata).* In the dioecious individuals of other species, however one of the gametophytes is a male one and develops *antheridia* the other is a female one; thus the individuals, the gametophytes are sexually entirely differentiated, but the zygote is hermaphrodite. It is an important development here, that the wall of the zygote is thickening, becomes surrounded by cortical cells; we might even state that it transforms into a *sporangium,* because in its interior by reduction division haploid cells arise, which are entirely homologous with the spores of vascular plants. This phenomenon starts a new developmental trend in the vegetable kingdom, which began to materialize progressively at the beginning of terrestrial life in the developmental stage of the Mosses, probably already in the Cambrian.

Thus for the fresh-water filamentous algae it can be established that the three developmental stages appear according to the same pattern as has been observed in the unicellular organisms, since in the distribution of the reproductive organs again monoecious, dioecious and dioecious heteromorphous individuals originate. The zygote is still unicellular, but already exhibits physiological differences (isozygotes, homozygotes and anisozygotes respectively). It is a further important circumstance that these three developmental stages equally occur in the monopodial *Siphonocladales,* in the dichotomous Siphonales *(Vaucheria)* and in the *Drapalnaldia* and *Drapalnaldiopsis* of verticillate branching from which again the probable inference may be drawn that the origin of the fresh water Algae might have been polyphyletic right from the start as unicellular organisms. This cell-filament stage must have been realized in the Praecambrium and Cambrium age of the Earth. From that age a great number of filamentous Algae remains came to light and which developmental grade was preserved by many fresh-water filamentous algae until our days.

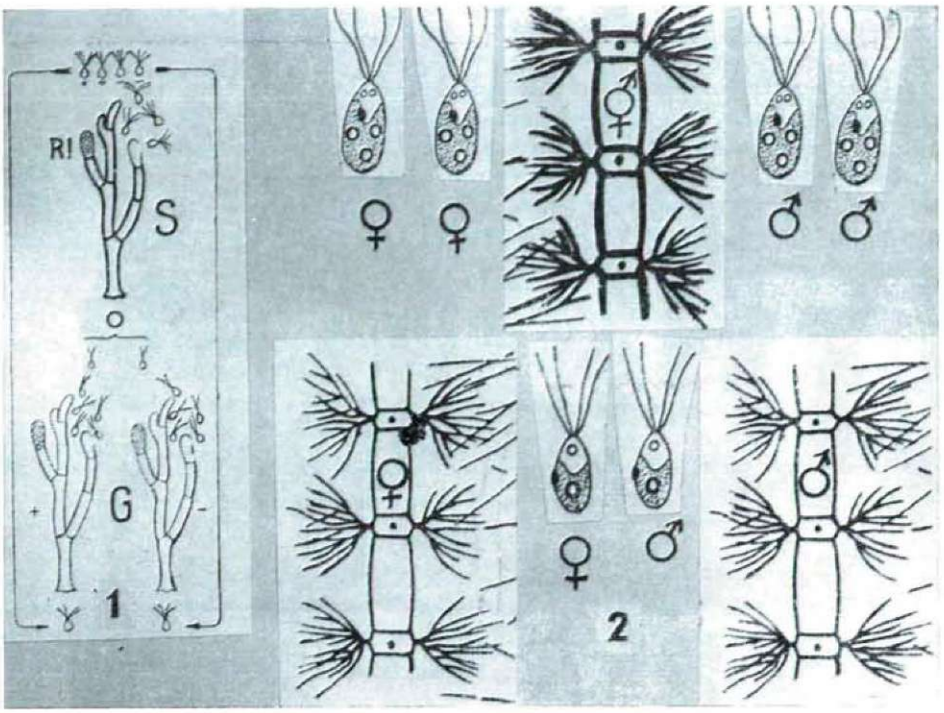


Fig. 14. Homomorphous alternation of generations in *Cladophora glomerata (Siphonocladales).* The gametophyte (G) is dioecious, morphologicaly entirely identical with the diploid sporophytic phase. This is one of the initial phases of the transformation into multicellular of the diploid phase.

An entirely similar change of generations is found in the development of *Drapalnaldiopsis indica.* The gametophyton filaments of male and female character develop gametes of male and female character from the fusion of which a hermaphrodite sporophyton entirely similar to the gametophyton arises. In the individual cells of these by reduction division 4 ciliate male or female swarming spores develop.

Stage VI. Bryophyta and Charophyta

After having examined the patterns of reproduction and the phylogeny of the *Thallophyta* s. l. we propose to review the position in the terrestrial and aquatic cormophyt plants. In these the manifestation of sexuality and the so-called alternation of generations which was rather concealed in the organisms dealt with so far-, becomes more explicit and conspicuous. Essentially, however, the picture is the same, since both among the liverworts and the *Musci* there are also individuals whose reproductive organs — here already well developed *antheridia* and *archegonia* — either develop on the same individual, so that the individuals are again *monoecious,* and accordingly the spores are both from the morphological and the physiological point of view completely equivalent i. e. isospores, or the individuals are *dioecious* and accordingly the spores are,

though morphologically identical, physiologically different, i. e. *homospores*, or there are morphological differences, consequently sexual dimorphisms even among the spores and individuals of the dioecious individuals and accordingly the spores are anisospores.

Isospore and isosporangium.

The spore from which only one kind of moss-individuals arise is called *isospore*, while the sporophore in which the isospores originate: *isosporangium (isosporogonium)*. Generally in the following all reproductive cells which develop by reduction division i. e. asexually and always at the end of the asexual process or before the beginning of the sexual process, will be termed as spores. In the Mosses the sporophytic phase originating the spores and the *sporangia* that develop on them are both morphologically and physiologically completely similar to each other and thus *isosporangia*. In the most primitive form in these *isosporangia* only such spores develop as carry in themselves both the male and the female character, so they are actually hermaphrodite spores. In these hermaphrodite spores the sexual chromosomes determining the sexual character are present though but not separated yet from each other, since in all spores originated both sexes or the DNA determining the sexual character are present at an equal rate and separation only begins when on the monoecious in this case the *sporangia* are *isosporangia* and the spores developing in them gametophytic generation the reproductive organs — *antheridia* and *archegonia* — develop on the same structure or on little separate branches. Consequently *isospores* (Fig. 15. 1).

This phenomenon also essentially coincides with the condition in which in the unicellular organisms within the single zygote cell two types of individuals, gametes arise, or when on the same individual of the filamentous Algae equally male and female types of gametes develop; the cell filament is thus monoecious. In all three periods of evolutional history the essence of monoecism is the same, although in the multicellular filamentous Algae and *Charophyta* this is somewhat more developed than in the unicellular organisms, while in Mosses the same condition appears as a consequence of the more developed alternation of generations in a still more advanced form.

Homospore, Homosporangium.

In Mosses the next developmental stage of sexual differentiation is when one spore is not sufficient to create progeny but the fusion of two sexual cells originating from a male spore and from another, female spore is necessary. Although the spores of such dioecious Mosses are morphologically quite identical, physiologically they exhibit significant differences. In the homospores the sexual character extends from the sexual chromosomes to the whole gametophytic generation, subsequently to the spores but not yet to the *sporangia*. The spores are separated from each other for the time being only cytologically (physiologically) and only in the sexual chromosomes, but not morphologically so far. The external appearance of the spores and gametophytes is entirely

similar; so is the form of the *sporangia* on the sporophyte, but in such similar *sporangia* already two kinds of spores, so called *homospores* arise, half of which (50 per cent) carries completely male character while the other half (50 per cent) is of completely female type. So in this case in the dioecious Mosses the sporophytic stage is completely similar, the *sporangia* morphologically continue to be *isosporangia* but essentially, together with the spores, they are already physiologically different, i. e. *homospores* or *homosporangia* respectively (Fig. 15, 2).

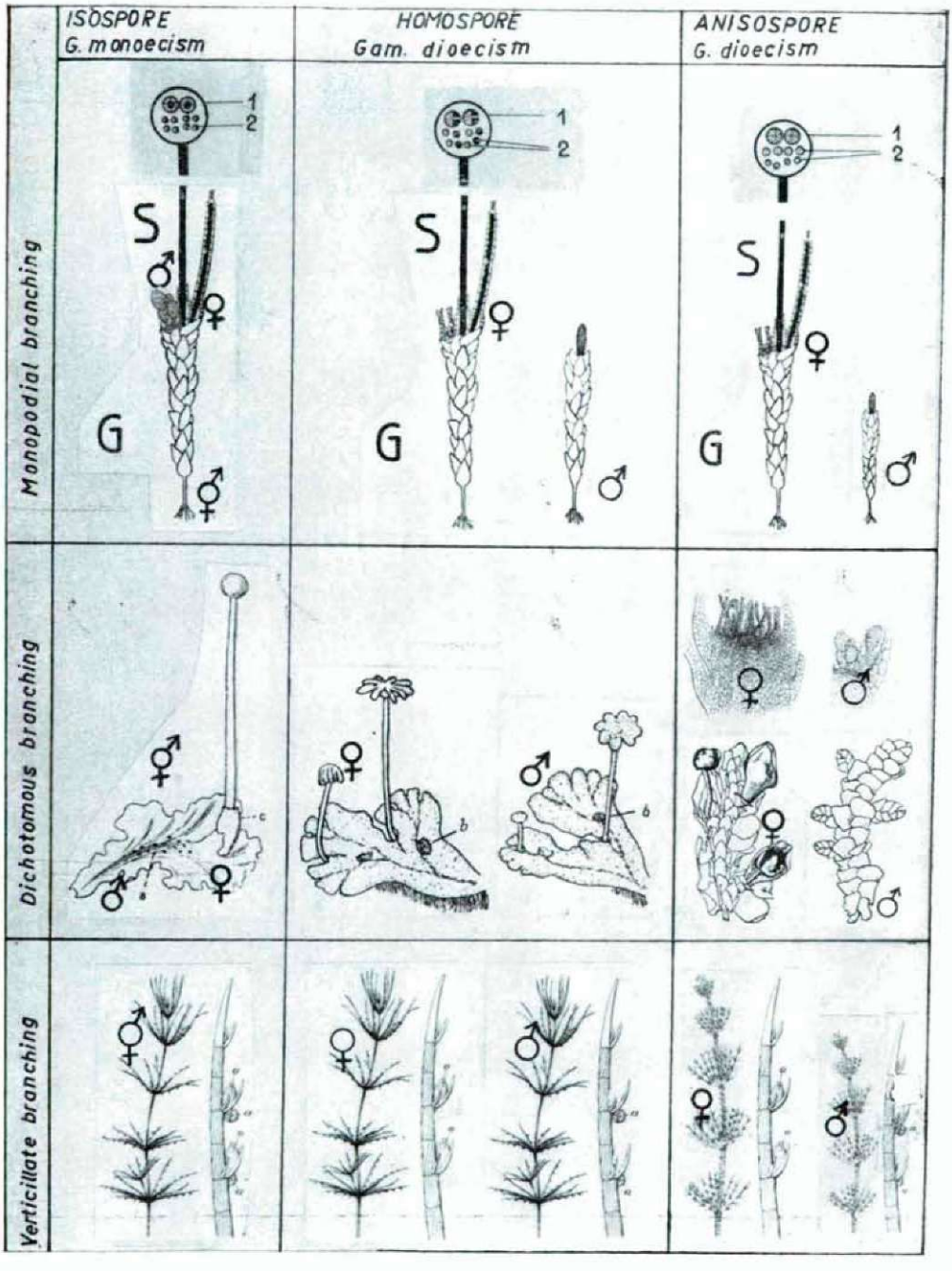
Also these conditions entirely agree with those observed in the unicellular organisms producing homogametes as well as with Green *Algae* species developing homoindividuals and homogametes. The essence is the same, the regularity in monoecism and dioecism remains unchanged.

Anisospore, Heterospore, Anisosporangium.

A still higher degree of evolution, of sexual differentiation is realized when the spores originate in the same *isosporangia* completely similar to each other but already a sexual dimorphism arises under them, since in reduction-division when the tetrades come into being always two bigger, so called *macrospores* and two smaller *microspores* take their origin, i. e. the microspores of male and the macrospores of female character develop in the same *sporogonium* (Fig. 16). Thus in the evolutionary history of Mosses the sexual, morphological differentiation made a further step, extending now to the spores representing

Fig. 15. *Isospore, homospore* and *anisospore, monoecism, homomorphous dioecism* and *heteromorphous dioecism* among *Musci, Hepaticae* and *Characeae*. 1. row. On the gametophyte of monoecious *Musci* the male-type *antheridium* and the female-type *archegonium* are on the same gametophyte. The diploid phase is monoecious, in the *sporangia* at reductiondivision hermaphrodite-type *isospores* develop, both the gametophyte and the sporophyte are monoecious. 2. Homomorphous dioecism, homospore. From the morphologically similar but physiologically different homospores gametophytes of similar form but of male and female type develop; the spores are *homospores*. On each of the monoecious sporophytes at reduction-division two homospores of different sex develop which are morphologically similar but physiologically different.
3. *Anisospore*. From the smaller male-type microspores smaller dwarf males, while from the larger spores *(anisospores, macrospores)* larger female-type gametophytes and on these *archegonia* develop. From the fertilization monoecious sporophytes arise in whose *sporangia* male type *microspores* and female type *macrospores, anisospores* develop, exhibiting different sizes and physiological differences. The *sporangia* are isomorphous, *isosporangia,* whereas the spores developing in them are of three different types viz. *isospores, homospores* and *anisospores*.
2. row. Among the dichotomously branching *Hepaticae* again monoecism e. g. *Pellia epiphylla,* homomorphous dioecism e. g. *Marchantia polymorpha* and probably also heteromorphous dioecism occur. So both in the monopodially branching *Musci* and in the dichotomously branching *Hepaticae* the same developmental stage are found. Though the developmental stages are the same, the types of branching are different. *3. row. Chara fragilis* of verticillate branching. *Antheridia* and *oogonia* are found on the same individuum, consequently the plant is monoecious. On one individual of the dioecious *Chara aspera oogonia* only, while on the other *antheridia* only develop. Homomorphous dioecism. The male individual of *Chara crinita* carrying the *antheridia* is smaller than the female individuum; heteromorphous dioecism. Among the gametophytes of the branching and non-branching green algae the same three developmental stages monoecism, homomorphous dioecism and heteromorphous dioecism occur.

Stage VI. BRYOPHYTA and CHAROPHYTA



the sexual character. This developmental stage again completely corresponds to what has been found in the unicellular organisms in the case of dioecious anisogamy and in the similarly dioecious filamentous algae in the case of dioecious anisozygoty when morphologically different individuals developed from the same zygote *(Spirogyra, Bulbochaete)*.

Since the *sporangia* are morphologically still entirely equal, i. e. *isosporangia* (essentially *isogametangia*) but the spores developed in them not only physiologically but also morphologically differ from each other, so these spores, to distinguish them from the micro- and macrospores in the stirct sense of the word which should be dealt with later, are termed as *anisospores* (Fig. 15. 3).

The sexual differentiation of the spores — that has been observed hitherto in all living beings — is closely related to the biological law of the alternation of generations. The reference made to this phenomenon here is simply due to the fact that the alternation of generations appears in the Mosses in a very spectacular form.

In nature it is a general law — observed up to now in all cases — that the male sexual cells of the same individual are fertilizing the female-type cell only in the very worst case, since heterofertilization is always more successful from the viewpoint of the evolution of species. Morphological and physiological differentiation of gametes and spores is invariably the realization of this biological law.

Let us now review the pattern of realization of these four developmental stages *isospore, homospore, anisospore* and *heterospore)* within the Mosses. The phylum of the Mosses comprises the two classes *Musci* and *Hepaticae* (liverworts). The *Musci* generally present monopodial while the liverworts more dichotomous branching. Both in *Musci* and *Hepaticae* the same kinds of spores and the same developmental stages occur, i. e. *isospores, homospores* and *anisospores*. From *Musci* e. g. in *Bryales* within 466 genera about 13 334 species were found according to our investigations. From these 114 genera (24 per cent) are *strictly monoecious* (isosporous) and 242 genera (52%) strictly

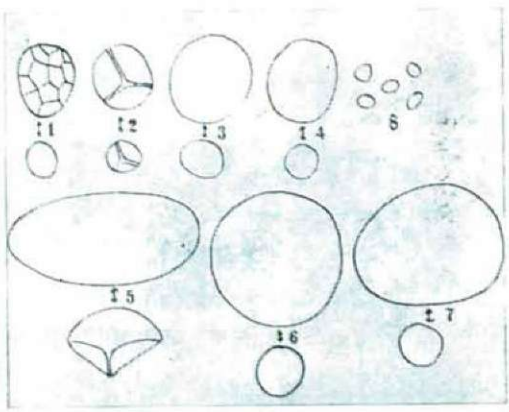


Fig. 16. The anisospores of some *Musci*. The anisospores of 1. *Sematophyllum piliferum*. 2. *Fontinalis antipyretica*. 3. *Antitrichia curtipendula*. 4. *Endotrichella elegans*. 5. *Pterobryopsis cochlearifolia*. 6. *Phyllogonium viride*. 7. *Macromitrium Blumei*. 8. *Dawsonia superba* homospores are morphologically equal, but physiologically different.

dioecious, (homosporic) and 110 genera mixed (24 per cent) i. e. occurring both in monoecious and dioecious (isosporic or homosporic) forms.

Among the *Hepaticae* dioecious species with special anisospores are rather frequent. So are e. g. the members of the genera *Fontinalis antipyretica* or *Macromitrium* where the diameter of the macrospores is at least four of rive times as large as that of the microspores (Fig. 16). As a contrast in the similarly dioecious Muscus *Dawsonia superba* all spores are exactly of the same size, so they are homospores. Another phenomenon occurring in Mosses is that in one of completely similar *sporangia (isosporogonia)* macrospores develop for the most part, while in the other microspores prevail. Moreover, in the same individual of *Brachymonium barbe montis* (Mexico) *sporangia* of two different sizes and in these spores of two different sizes are found; these are already essentially materialized *microsporangia* or *macrosporangia*. Or in the exa mined 39 *sporangia of Fontinalis antipyretica* two different sizes occur, the length raning between 4,72 and 2,65 while the wide between 1,62 and 0,92 mm. This is already a developmental stage which to a greater extent and a more explicit form is realized on a higher level than that of Mosses in the phylum of Pteridophytes *(heterosporangia)*.

Essentially similar conditions are encountered in the class of the dichotomously branching *Hepaticae*, where also both the monoecious *(Pellia)* and — mainly — the dioecious condition is found *(Marchantia)*. Although no anisosporous phenomenon was observed, still, in our opinion, it must occur, since it is a necessary stage in phylogeny.

VI. b. Charophyta

Conditions completely identical with those found in *Bryophta* occur also among the "most developed" fresh water green algae, the *Characeae*, which with their comparatively highly developed threedimensional cellular structure do not fit at all in the fresh water filamentous green algae, although the principle of the construction of their body essentially agrees with the organism of the green alga *Drapalnaldiopsis indica*. The highly developed gametophytes of the *Characeae* and their reproductive organs, *oogonia* and *antheridia*, of the same developmental stages are much nearer to the developmental stage of *Hepaticae* or *Musci* than to the simple filamentous algae. On the strength of these and of other weighty arguments, in our opinion — strange as it may sound — *Chara* ought to be definitely removed from the fresh water filamentous algae and should be rated as a class of the same rank as *Bryophyta*, as a class in which the gametophytes are much more developed than the sporophytes, with reproductive organs much more developed than those of the filamentous green algae and essentially similar to those of the Mosses *(antheridia* and *archeogonia* or *oogonia)*. In view of these important characters the objection dwindles away that the sporophyte of the *Characeae* as againts the huge gametophyte is shrivelling into a unique cell, the zygote. When taking only this feature into consideration *Chara* really ought to be relegated in the green algae with cell filaments. The multicellular cell-bodied gametophyte and the structure of the highly developed multicellular *antheridia* and *oogonia* are, however, much more comparable with the similar organs of *Hepaticae* and *Musci* than to the

reproductive organs of the fresh water algae with cell filaments. There is a great similarity, however, not only in this respect but also as to the distribution of the reproductive organs, viz. with the monoecism, dioecism and heteromorphous alternation of generations in Mosses.

Summarizing the above statements on the distribution of the reproductive organs, we want to make it clear that the same conditions occur here as in the unicellular organisms. To isogamy corresponds the *isospore*, to homogamy the *homospore* and to anisogamy the *anisospore* or essentially heterospore respectively. Another important finding is that *Musci* and *Hepaticae* are on the same developmental level, since both are Bryophytes and in both the isosporous, homosporous and anisosporous conditions equally occur. The *Musci*, however, exhibit monopodial, while *Hepaticae* more frequently dichotomous branching. Since these two kinds of branching can not be derived from each other, we may draw the same inference as we did in the case of the unicellular organisms and of the Algae, namely that also Bryophytes, similarly to the organisms dealt with hitherto, are of polyphyletic origin. All these grades of the history of evolution were attained by the flora in the palaeszoic age of the Earth, in the Silur, i. e. in the Ordovicium or Gotlandicum, about 400 million years ago.

Stage VII. Psilophyta

As a consequence of the adaptation of the vegetable kingdom to terrestrial life the moss stage made a further progress. The sporophyton phase hitherto vegetatively or physiologically not independent from the air, from the top of the gametophyton gradually came into contact with land, started a more intensive growth and became now able to lead an independent life at the

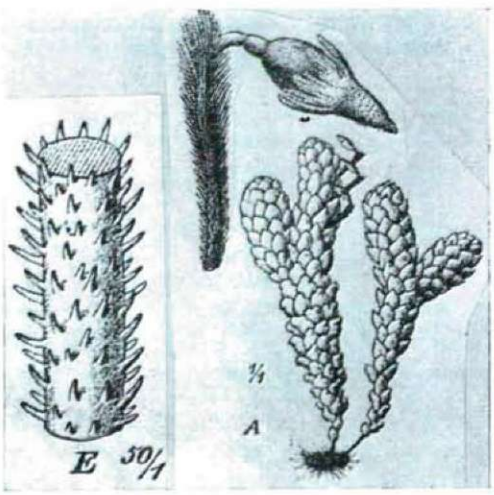


Fig. 17. On the sporophyte of *Eriopus cristatus* there are assimilating *paraphylla* promoting its physiologically independent life. From the surface of the sporophyte of *Lepidopilum subsubulatum* similar epidermal structures, emergencies arise as from the surface of the stem.

expense of the gametophyte. One of the results of this process was that in the hitherto non-branching sporophytic generation tiny assimilating leaves *(microphylla)* developed from which some, particularly towards the apices of the little stems, contributed to the origin of the *sporangia.* This is how on the vascular plants gradually the *sporangium* and *sporophyllum* stage developed.

This developmental stage is seen to materialize among the *Musci,* e. g. in the Australian species *Eriopus cristatus* on the sporophyte of which assimilating *microphylla (paraphylla)* developed, while from the base of the sporophyte root hairs originated (2 n!) or in the fossile primitive shrubs *Psilophyta* and their progeny the *Pteridophyta.* Already the ancient primitive skrubs the Psilophytes of the Cambrian and Silurian to all probability carried isospores or homospores respectively, whose *sporangia* developed partly on leaves, on the so-called *sporophylla* or were located on the top of the leafless stem or at its side in the axil of tiny leaves. We refer to probability, because the Psilophytes are not sufficiently known, so that it is open to discussion whether their sexual generations were monoecious or dioecious. There is no doubt, however, that they must have existed, since their spores are known, and from these only haploid monoecious or dioecious *prothallia* could have developed. According to recent investigations the rhizometype part of *Asteroxylon, Rhynia* in the earth as a matter of fact does not belong to the sporophyte sector but to formallity alike the gametophytic generation and could have presented an analogy to the homomorphous development of *Cladophora* referred to in connection with the Algae. What so ever the *prothallia were,* among the sporophytes (2 n) similarly to the previous findings 3 main types of branching can be distinguished, namely the *monopodial (Rhynia, Hornea),* the *dichotomous (Protopteridium)* and the verticillate (whorled branching (*Calamophyton,* Fig. 18). So in this period again the identical developmental

Stage VII. PSILOPHYTA

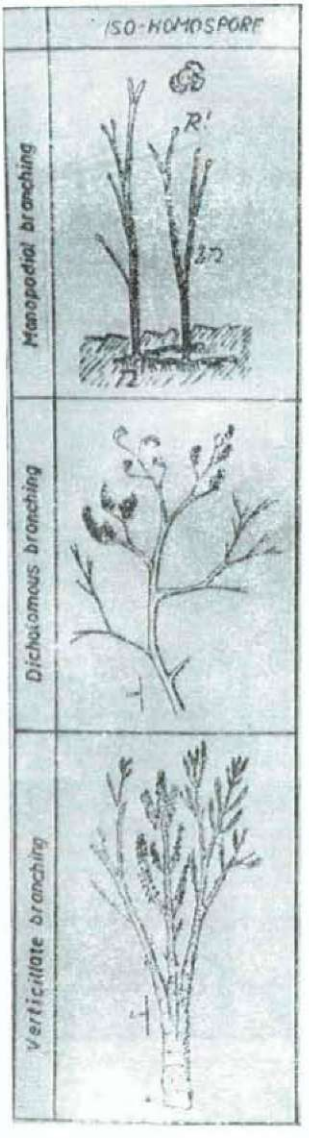


Fig. 18. The gametophyte (n) and sporophyte (2n) of the monopodially branching *Rhynia* are more or less of the same form. The gametophyte might have developed from isospore or homospore. (1) The sporophyte of the dichotomously branching *Protopteridium* must have developed similarly from isospore or homospore. (2) The sporophyte of *Calamophyton* of the verticillate type of branching too are derived from isospores or homospores. Again identical developmental stage and 3 types of branching side by side.

stage of the spores and simultaneously the three forms of branching appear at the same time. The terrestrian flora reached this developmental degree in the history of Earth in the Devonian, the recent representatives of which evolutionary stage are *Psilotum* and *Tmesipteris.*

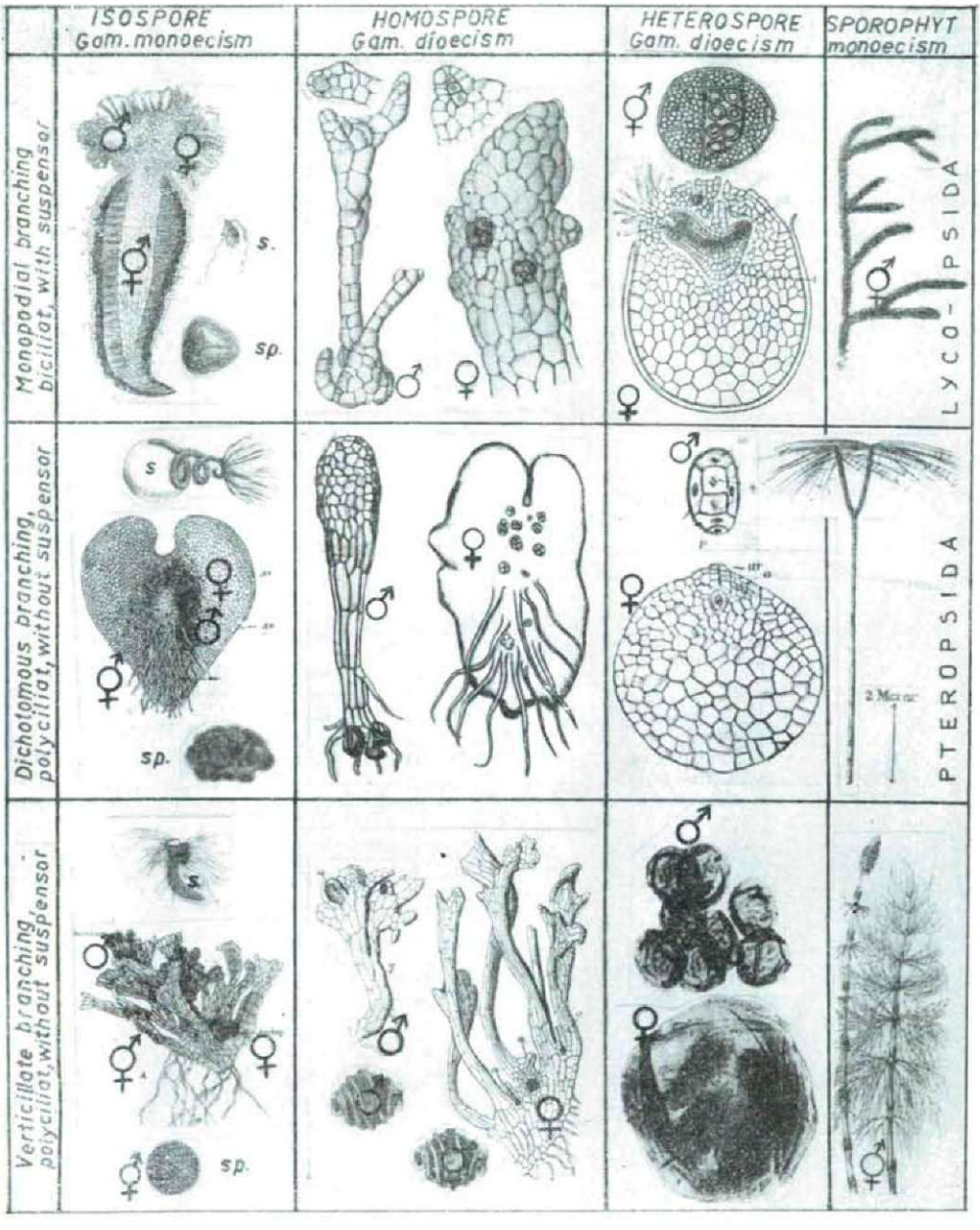
Stage VIII. Pteridophyta

Isosporophylla. Among the Pteridophytes in the strict sense of the term evolution advances further, since at on the macrophyll beneath of the sporophyte *(Filicinae)* or in the *sporangia* of the microphyllous sporophyte *isospores (Lycopodium)* or in the somewhat more developed form of the latter homospores *(Equisetum)* develop, while in others in the same *sporangium* already micro- and macrospores, i. e. heterospores *(Marsilea)* and finally in the most developed stage on the monoecious or dioecious sporophyte in the differentiated *microsporangia* only microspores and in the *macrosporangia* only macrospores formed *(Selaginella)* and either in one common or separate so-called (macro-sporophyllous or microsporophyllous *strobiles.*

Where do these stages of sexual differentiation, the *isospores, homospores* and *heterospores* appear within the *Pteridophytes?* The *Pteridophytes* are ranged in three great classes: *Lycopsida, Pteropsida* and *Sphenopsida.* To *Lycopsida* belong the *Lycopodia* and *Selaginellae,* to *Pteropsida* the *Filicinae, Hydropterides* and *Isoetales,* while to *Sphenopsida the Equisetum* sp. and the fossile *Chalamites.* The stem branching of the microphyllous *Lycopsida* is generally monopodial, while the terminal branchings of the conductive bundles and ribs of the macrophyllous *Pteropsida* are nearly always dichotomous and the *Sphenopsida* exhibit a typical verticillate branching. A study of these three

Fig. 19. Monoecism-dioecism and heteromorphous dioecism in the *prothallia* of the *Pteridophyta (Lycopsida, Pteropsida, Sphenopsida).*
1. From the isospore of the microphyllous *Lycopodium clavatum* of the monopodial type of branching a monoecious *prothallium* originates.
2. From the homospore of *Lycopodium sp* a female-type macrospothallium and a male-type microprothallium of smaler size develops.
3. From the microspore of the similarly monopodially branching microphyllous *Selaginella* male-type, while from the macrospore female-type *prothallia* develop (heteromorphous dioecism).
2. row. From the isospore of the macrophyllous *Dryopteris filix mas* a monoecious *prothallium* originates, while from the homospore of *Ceratopteris thalyctroides* a dichotomously branching female-type *macroprothallium* and a male-type *microprothallium* of smaller size develop. The spores are morphologically analogous but physiologically different, i. e. homospores. From the microspore of the polyciliate *Isoetes lacustris* a maletype *microprothallium,* whereas from the macrospore a much more developed female-type *macroprothallium* develops.
3. row. From the isospore of *Equisetum* only one bisexuell sort of *prothallium* (after SCHMIDT) from the homospore of *Equisetum arvense* fifty per cent female-type and fifty per cent male-type *prothallia* originate. From the macrospores of *Paracalamostachys striatus* of the Carboniferous, a plant of verticillate branching, female type *prothallia* originated, while from the microspores male-type *prothallia.* The upper row is characterized beside the spore types by monopodial branching, biciliate spermatozoid and a suspensor on the embryo. All these properties are phylic features and seem to evidence that the three phyla *Lycopsida, Pteropsida* and *Sphenopsida* developed independently from each other and concurrently until the heterosporous stage.

Stage VIII. PTERIDOPHYTA



main types as to the location of their spores and reproductive organs in general reveals that in all three types the isosporous, homosporous and heterosporous developmental stages exist. But the same conditions were found in the characteristic forms of the Carboniferous, namely in the monopodially branching *Lepidodendron,* in the dichotomously branching *Sigillaria* and in the verticillately branching *Calamites.*

Thus within the *Pteridophytes* again the same developmental stages, sexual differentiations and the three main types of branching appear as in the unicellular organisms, the *Algae, Mosses* and primitive shrubs: namely the gametophytes of the *Pteridophyta* too are either monoecious or dioecious, while the sporophytes are still exclusively monoecious.

In recent ferns e. g. in *Selaginella* the sexual conditions are probably much the same as in the Lepidodendrous which liver in the Carboniferous. Both spores of *Selaginella* from the same strobile drop at ripening to the earth where fertilization can take place only through water as a medium. Inspite of the high degree of differentiation in the flora of the Carboniferous sexual propagation was still linked with the temporary presence of liquid water. In the phylogeny of the vegetable kingdom and particularly in the development of terrestrial vegetation it was the most important period when the vegetable kingdom made itself independent from the presence of liquid water at fertilization; this developmental stage had set on in the Carboniferous. According to our present knowledge in the Carboniferous both the macro- and microspores

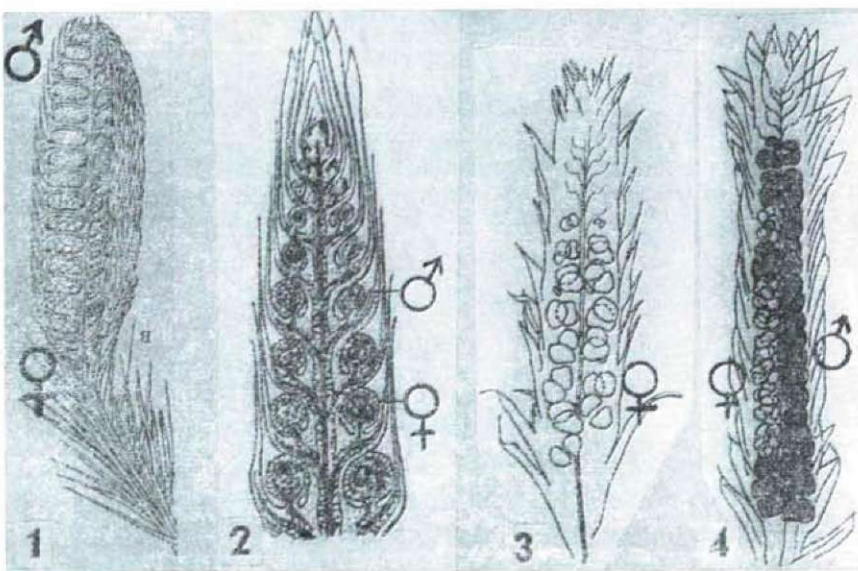


Fig. 20. In the sporophyllic string of *Lepidodendron* below in the *macrosporangia* the macrospores and in the *microsporangia* the microspores are localized. This strobile structure points to monoecism. (1) Exactly the same structure is found in recent monoecious *Selaginellae* (2) or in the strobile of the fossile *Calamites* which are of the same age the *Lepidendrons.* In the strobile of *Selaginella* sp. are only macrosporangia localized (3), on other *Selaginella* species the macro-and microsporangia non separately one above the other, but side by side are localized. (4).

from the strobiles of *Sigillariae Lepidodendrons* and *Calamites* still roppen to the earth, possible on banks, where they germinated, and fertilization also took place on the earth through the medium of liquid water. The embryo which came into being after fertilization continued its development on the earth, as a rule in a moist environment.

Stage IX. Pteridospermae

Isospermia, Homospermia. The change of this stage was marked by the phenomenon, that the *macrosporangia* did no more drop on the earth, on the banks, but remained connected with the mother plant until the fertilizing sexual cells (microspores) were carried no more by the water but by the wind within easy reach of the *macrosporangia*. Thus the act of fertilization has been again raised into the air, on the sporophyte, where the role of the water has been now taken over by the wind. The result of fertilization on the sporophytic mother plant in the air became a new structure, the *seed*, which dropped to the earth only after nutrition by the sporophytic mother plant and a certain development, and which organ now already represented all properties of both parents, the same as the zygotes of the unicellular organisms or of the multicellular algae or the sporophytes of the *Pteridophyta*.

Stage IX. PTERIDOSPERMAE

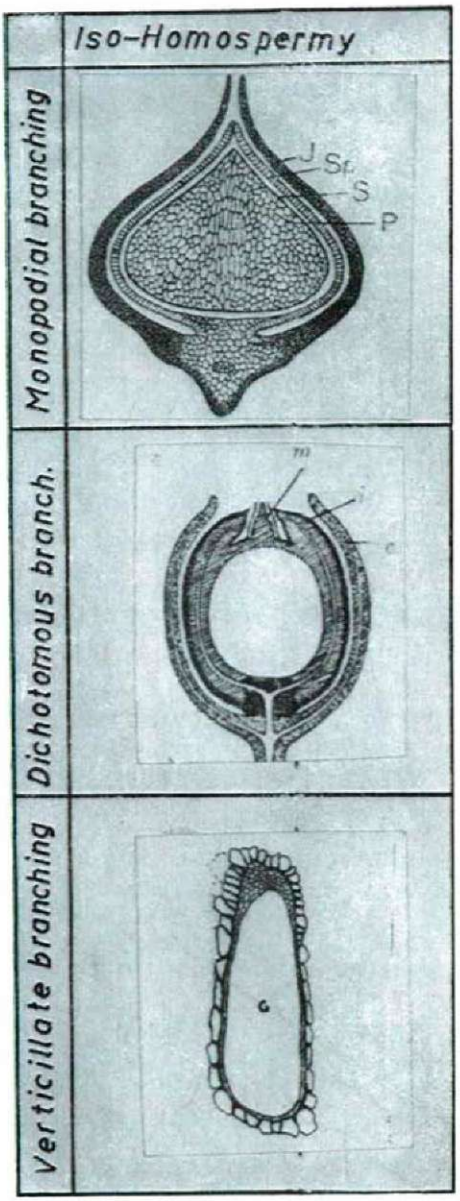


Fig. 21. 1. The structure of the ovule in *Lepidocarpon lomaxii* (microphyllous type). To all probability it has been monoecious.
2. The open ovule of *Lyginodendron Oldhamium. (Pterispermae).* (The mother plant was probably dioecious.)
3. The macrospore of the recently discovered verticillate *Calamocarpon insignis* (BAXTER) and in it the gametophyton (G). All three are *Pteridospermae* and represent the three main branching types on the identical degree of development.

Since in these primitive *Pteridospermae* in separate *sporangia* microspores and distinct macrospores developed which might have developed separately but also in the same strobile, so the sporophytes were monoecious, but they might have also developed in different strobiles and either on the same individual when they are monoecious (Fig. 22) or on different individuals when the sporophytic generations became dioecious. With this further step the sexual dimorphism now extended from the gametophyt to the sporophytic generation, and so gradually monoecious and dioecious terrestrial Spermatophytes began to develop. In the history of evolution of the vegetable kingdom, this high degree of morphological sexual dimorphism obtained a decisive importance in the conquest of the mainland, because the sporopherous vascular plants gradually began to develop into Spermatophytes. No essential change occurred in the mutual relationship of the two sexes, because the primitive Spermatophytes also continued to be either monoecious or dioecious.

According to our present knowledge the development of seed materialized within the Pteridospermae at least in three directions *(Lyginodendron, Lepidocarpon* and *Calamocarpon)* (See Fig. 21.) why the seedlike megasporangia of the verticillate branching is discouvered recently by BAXTER. The realization of this evolutionary degan about 320 million years ago in the Carboniferous.

Stage X. Gymnospermae

The further transformation of high importance was initiated by the condition that the *macrosporangia* of female character in the aments and on the *macrosporophylla* remained free for the time being and thus were exposed to rather manyfold dangers. Gradually the *integument* enclosing the *macrosporangium* (Fig.) began to provide for their protection, but the *macrosporangia* did no more drop on the ground for the period of fertilization where hitherto the liquid water was the medium of fertilization. This intermediary role has been assumed now in the air by the wind. Since these primitive ovules developed from the *macrosporangia* when they were still free, the seeds which came into being after fertilization also remained open. This is how the first Gymnosperms came into existence. Let us see, by what means?

The formation of Spermatophytes.

It has been shown on the recent *Selaginellae* and on the fossile Lepidodendrons that in the same strobile there are or were both *micro-* and *macrosporangia* together. From this sporous condition the gymnospermous condition could have come into existence by means of development in some individuals in the individual mixed strobiles gradually either into macrosporophyllous strobiles only, while in others to microsporophyllous, strobiles or aments only. Thus the mixed strobiles gradually began to transform into unisexual ones and by this phase the sexual dimorphism extended to the strobiles. Such primtive condition occurs even today in some individuals of recent *Selaginellae (Selaginella apus* et c.) but, to all probalility, the same thing happened with the most developed ferns of the Carboniferous, the *Lepidodendrous* or *Pteridо-*

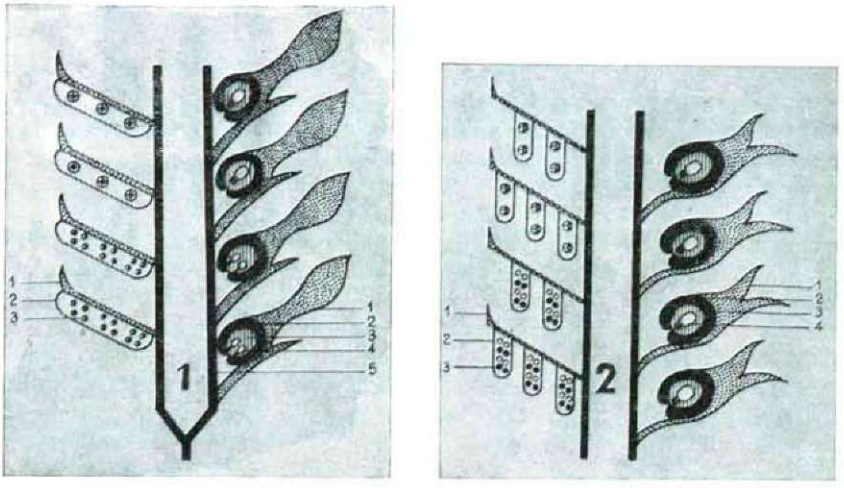


Fig. 22. Distribution and structure of the strobiles of the monoecious (isospermy) and (homospermy) dioecious Gymnosperms.

spermae. Since both sexual characters were inherent in the sporophytic generation, the segregation of sexuality extended either to some branches of the same individual and hereby the monoecious gymnospermous Spermatophytes came into existence, or one of the sexual character depressed the other so far that only that one could assert itself particularly, namely the male or the female character only, and as a result two kinds of sporophytous Spermatophytes, i. e. dioecious plants came into existence. The other sexual character did not cease to exist in these plants entirely because it continued in latent state in the apparently unisexual sporophyte. This is why in the male individuals of some dioecious Spermatophytes female characters, while on the female individuals male characters could appear, e. g. in some aments of Gymnospermous plants carpels develop and vice versa *Pinus)*.

Isospermy, homospermy. Sporophyllum strings, aments, strobiles, dioecious and monoecious spermatophytous condition.

After the monoecious and dioecious ferny stage only the gymnospermous spermatophytous could have succeeded, either in the monoecious or in the dioecious form. Monoecism and dioecism are both spermatophytous conditions though among the Gymnosperms, but there are very essential physiological differences between the seeds because tho one kind of seed produces only one kind of individual, namely a monoecious plant, a sporophyte, while the other develops two separate individuals, sporophytes i. e. dioecious plants. In the unicellular organisms, in filamentous Algae, in Mosses and in the Pteridophytes too, we observed that from the isospores only one kind and from the homospores (zygotes) two kinds, namely individuals, gametophytes of male and female character develop. Exactly the same conditions continued to prevail also in the monoecious and dioecious gymnospermous Spermatophytes. In

these no several different cases can occur either. Therefore on account of the analogy or identity with the previous forms we may term the seeds of the monoecious Gymnosperms as isogymnosperms and those of the physiologically different dioecious as homogymnosperms, since from the point of view of sexuality there is the same cytological i. e. heterochromosomatical difference among them as among the isogametes, isozygotes, isospores and among the homogametes, homozygotes and homospores. Here, as in all other cases, the sexual differences are caused by the heterochromosomes as invariably evidenced beyond doubt by cytological examination. This might also explain the fact that e. g. in some dioecious *Cycadales* the chromosome number is 8 or 9, depending on whether male or female individuals were examined and which specimen was heterozygotic. In this connection the question arises by what means these monoecious and dioecious conditions i. e. *isospermy* and *homospermy* materialized in recent and fossile *Gymnospermae* and *Chlamydospermae*. These gymnospermous Spermatophytes are also either monoecious or dioecious, but several types may be distinguished among recent and fossile Gymnosperms. The dioecious *Ginkgoales* and *Cycadales* belong here, but can be relegated to them. A closer examination of these forms reveals three main types of branching in the stems, branches and in the terminal branching of the conductive bundles of the ribs, namely among the monoecious *Coniferae* in the strict sense of the term the monopodial, among the dioecious *Cycadales, Ginkgo, Araucariae* and *Podocarpus* in the leaves dichotomous, and the mono- and dioecious *Cupressaceae* the opposite or verticillate branching.

Stage XI. Chlamydospermae

Similarly in the dioecious *Chlamydospermae* (Fig. 24), *Gnetum* represents the monopodial, *Welwitschia* the dichotomous (parallel) and *Ephedra* the whorled type of branching so that within the gymnospermous condition again the same developmental stages appear in each phylum which seems to indicate that the *Chlamydospermae* are not of homogeneous origin either; there is no doubt that they have reaced the gymnospermous state in the monoecious or dioecious form, proceeding from several types. Thus their origin is, similarly to the previous types, polyphyletic.

Stage XII. Angiospermae

The gradual evolution did not stop at the gymnospermous condition reached in the Carboniferous and Permian systems. Beginning from these periods gradually a new developmental stage materialized in the life of the vegetable kingdom. This transformation presents a change in the sexual reproduction pattern of the plants, substantiating at the same time the great adaptability of plants to the prevailing environmental conditions. This change became manifest in the first place by the phenomenon that the free *macrosporangia*, the so-called *ovules*, which on the *macrosporophylla* were covered by a thin integument, became now gradually covered by the edges of the sporophyllums. Hereby a completely new so-called *angiospermous* developmental stage arose,

Stage X. GYMNOSPERMAE

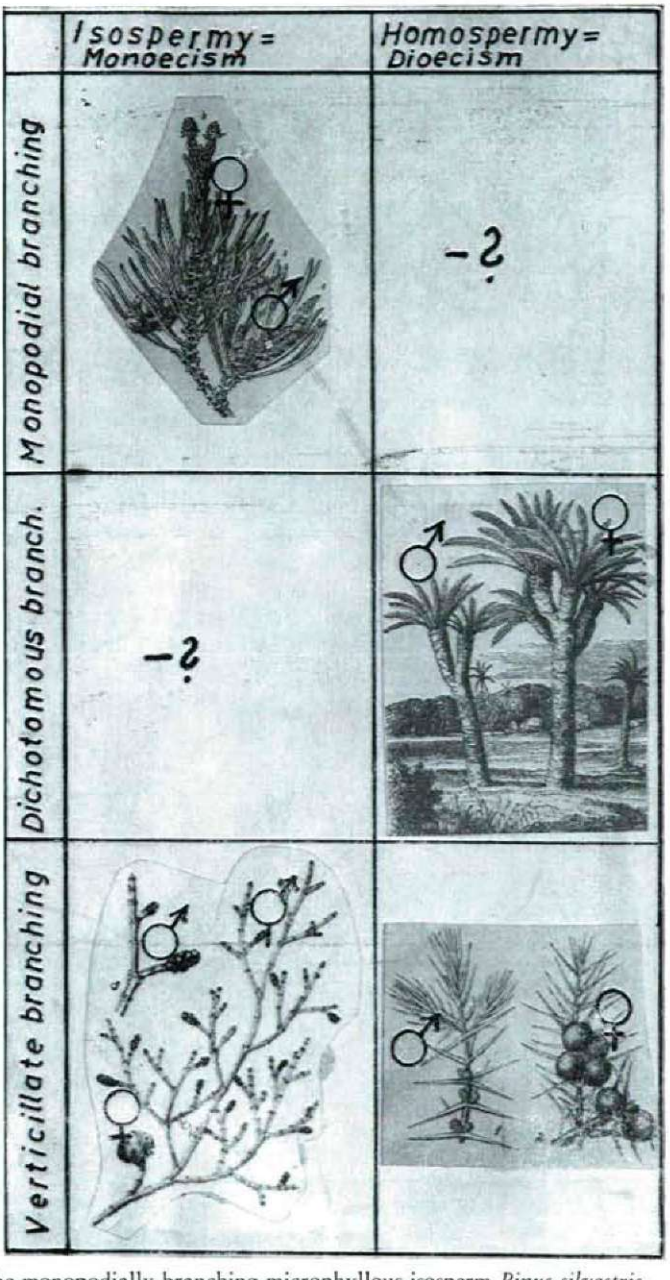


Fig. 23. 1. The monopodially branching microphyllous isosperm *Pinus silvestris.*
3. The verticillately branching of the isosperm *Tetraclinis articulata,* and of the homosperm *Juniperus communis.*
2. The macrophyllous dichotomously branching *Cycas revoluta.*
All three are Gymnosperms, but of three different types of branching.

Stage XI. CHLAMYDOSPERMAE

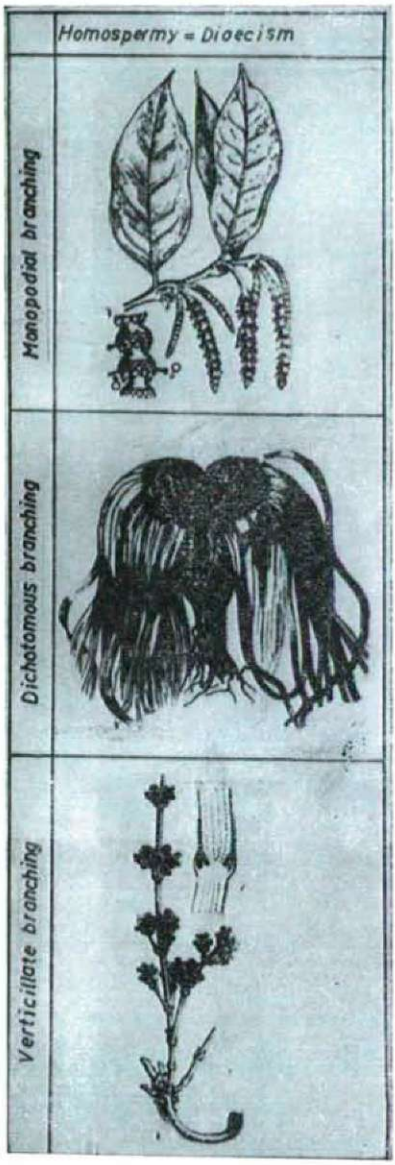


Fig. 24. 1. Gnetales, 2. Welwitschiales, 3. Ephedrales

when the so-called *carpel* entirely enclosed the thinly wrapped *macrosporangia*, the ovules, and thus the female reproductive organ assuring the survival of the species got into a completely protected position.

So from the *macrosporophyllum* gradually the pistil developed, the parts of which are the *ovary*, the *style* and the *stigma*. In this closed condition and high in the air even the temporary presence of liquid water became superfluous. By degrees the plants could do even without the wind, because from the early tertiary period the microspores (pollen grains) could be and were actually transported by the then widespread insects to the *macrosporophylla* of female character, to the pistils and in the first place to the primitive stigmas.

But even this did not happen at once, because this development had its degrees, too. What were these degrees? Similarly to the previous developmental stages also among the recent Angiosperms both monoecism and dioecism occur, but besides an entirely new form, the hermaphrodite or monoclinous flower makes its appearance. On separate branches of the same individual of the monoecious angispermous plants the strobiles of different sex, male aments and female flowers appear. Similarly to the cytological analogy of isogamy, isozygotes and isospores and to the term isosperm of Gymnosperms the seeds of the monoecious Angiosperms are named isosperm. On certain individuals of other species again we find only a male aments, while on other individuals exclusively female flowers. Such dioecious angiospermous Spermatophytes on the analogy of homogamy, homozgygote, homospore, homospermy might be named homosperms. Finally, from Angiosperms a particularly large number had reached the condition where in the same structure the reproductive organs representing both sexes are present together, i. e. both the *microsporophylla* which in this new structure are already termed *stamina*, and the *macrosporophylla* or pistils. At last, in the course of an evolution spanning thousand millions of years, the reproductive organs representing both sexes, the whole sexual generation, came close together on a single

sporophytic individual and within a single structure, the monoclinous flower. In the seeds of Angiosperms developing such monoclinous or hermaphrodite flowers the chromosome set of the cells, or at least the compounds involved in the formation of sexuality are present in another configuration than in the monoecious (isospermic) or dioecious (homospermic) plants and therefore, to distinguish them from the first two, they may be termed eusperms. Accordingly, the hermaphrodite condition of the sporophyte is the most developed stage reached by the plants starting from the unicellular condition during a development of many hundred million years, the forms of which we now encounter at all times and in all places. The hermaphrodite flower is, consequently, the highest stage in the history of evolution of the vegetable kingdom and it only could have developed according to the author's opinion — as demonstrated — from the unisexual strobiles. Let us examine, by what means this has been accomplished.

The origin of the hermaphrodite flower

This question is up to our days one of the most contested problems of the philogeny of plants. In our opinion, this latest monoclinous hermaphrodite condition could have developed only from the previous stages and from the unisexual flowers, because there was no other possibility in the Permian, Triassic and Jurassic periods. But even before, only two cases were possible, since among the primtive gymnosperms too only the monoecious and dioecious conditions existed so that only these could have been transformed into hermaphrodite flowers. But by what means? In our opinion, either by the development of *microsporophylla (stamina)* in the pistillate, i. e. macrophyllous strobilaceous flowers on the place of part of the carpels, e. g. at the bottom of the strobiles (pistils), by thrusting into the background the compounds eliciting female character. Thus the *stamina* and the pistils got next to each other and hereby became hermaphrodite flowers; or in the aments, e. g. on their top

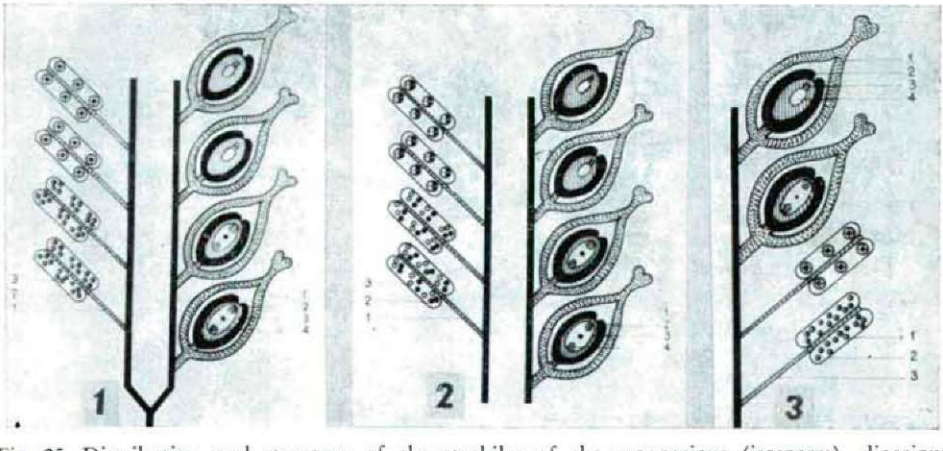


Fig. 25. Distribution and structure of the strobiles of the monoecious (isosperm), dioecious (homosperm) and monoclinous (eusperm) Angiosperms.

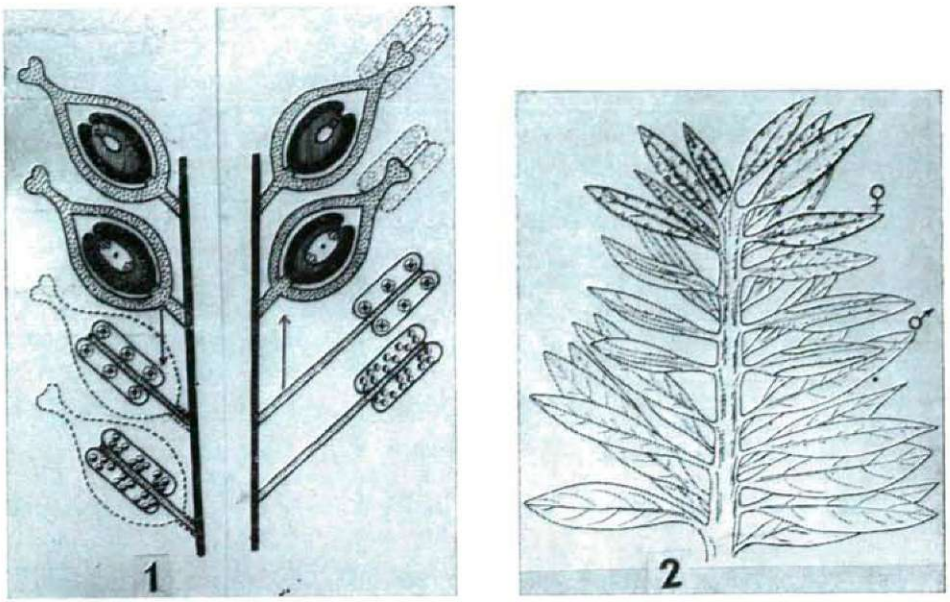


Fig. 26. The origin of the hermaphrodite flower. 2. Proangiosperm flower after *Hutchinson*. From under, upwards foliage leaws, after microsporophylla and macrosporophylla.

mainly pistillate flowers (pistils) came into being and this way the organs representing the two sexes got again next to each other and this could have been also a pattern for hermaphrodite flowers to develop. This process might have originated both in monoecious and dioecious gymnosperms, the more, since all sporophytes are essentially always hermaphrodite individuals in which the chromosomes and compounds determining the two sexes only separate from each other when partly the aments *(stamina)* and partly the carpels (pistils) originated. The probability of this assumption is enhanced by the fact that a similar phenomenon can be observed even in our days both in Gymnosperms and in Angiosperms. In the catkin of the willow tree e. g. frequently pistils occur among the *stamina* which shows that organs representing the two sexes can develop in the same structure quite close to each other and this way true hermaphrodite flowers come into being (androgynous aments). The same phenomenon can be observed, however, as an extraordinary occurrence, in maize, where from the middle of the tassel a pistiline strobile emerges with genuine ovules and seeds respectively. Similar phenomena are encountered in Gymnosperms *(Pinus)*.

In our opinion this process presents essentially the same general biological regularities which were observed hitherto in all developmental stages. The reproductive organs of our simplest monoecious and dioecious herbaceous Angiosperms invariably concentrated in monosexual strobiles similar to those of the Gymnosperms and particularly in male and female aments or coniform structures respectively. In the strobiles of both pheno- and genotypes always

the character representing the other sex, so both components of DNA were also present, but one of the component in latent condition, in the staminate aments the character determining the female sex and in the pistillate ament the character representing the male sex and the DNA respectively. Only upon the external and internal factors, so upon the contrasting configuration of DNA or upon the effect of the different hormones in one of the phenotypes one of the sexual characters appears while the other remains in recessive and latent condition as if in an expectant attitude. The development of the monoclinous flower must have started, in our opinion, always from such latent hermaphrodite condition, in a way that within the unisexual strobile, e. g. in the staminate ament, which may be considered essentially as an overmale individual, the female character hitherto depressed and in a latent, recessive condition, could have — as a result of the diminution of the male character — got gradually in a dominant position towards the apex of the ament. As a consequence the place of the upper *stamina* has been gradually more and more occupied by the female character — as one half of the intersex — that became more and more definite, while at the bottom of the strobile the old *stamina* continued to represent the male genotype. As a contrast in the pistillate ament that may be considered as overfemale, the male character, hitherto in latent condition, began in the bottom of the ament to transform also in its phenotype into stamina, i. e. to become dominant, so that in the final result the ament developed into a hermaphrodite flower. Essentially the same phenomenon is manifest here which has been demonstrated in the unicellular *Chlamydomonas eugametos*, when the unisexual individuals could be transformed by the influence of chemicals into individuals of the other sex.

This concept essentially agrees with the Euanthium theory according to which in the hermaphrodite flower the *stamina* should not be regarded as staminate flowers but as *microsporophylla* and the pistils not as female flowers but as *macrosporophylla.*

So within the Angiosperms we can distinguish monoecious, dioecious and hermaphrodite flowered individuals and these differences can be traced back to the different nature of the seeds, more exactly to factors determining sexuality.

It remains to examine how these developmental stages become manifest in the Angiosperms. The Angiosperms are divided in two great classes: *Monocotyledones* and *Dicotyledones*, both of which contain plants with monoecious, dioecious and hermaphrodite flowers. In the *Dicotyledones* monoecious, i. e. isospermic plants are e. g. the *Amentiflorae*, dioecious e. g. the *Salicaceae* and hermaphrodite generally the *Dialipetalae*. From the *Monocotyledones* e. g. the *Caricoideae* and *Palmae* are monoecious, the *Palmae* dioecious and the *Liliaceae* hermaphrodite.

As regards branching dicotyledons generally exhibit monopodial branching while monocotyledons — when taking into consideration the parallel nervure and also the branching of the stems in *Palmae, Dracaenoideae, Cordyline* etc. — rather more dichotomous. Finally when reallocating *Casuarina* to the Angiosperms, we will find also the third (whorled) type of branching represented. The essence is, however, that both in *Monocotyledones* and in *Dicotyledones* the same developmental stages, monoecism, dioecism and hermaphro-

Stage XI. ANGIOSPERMAE

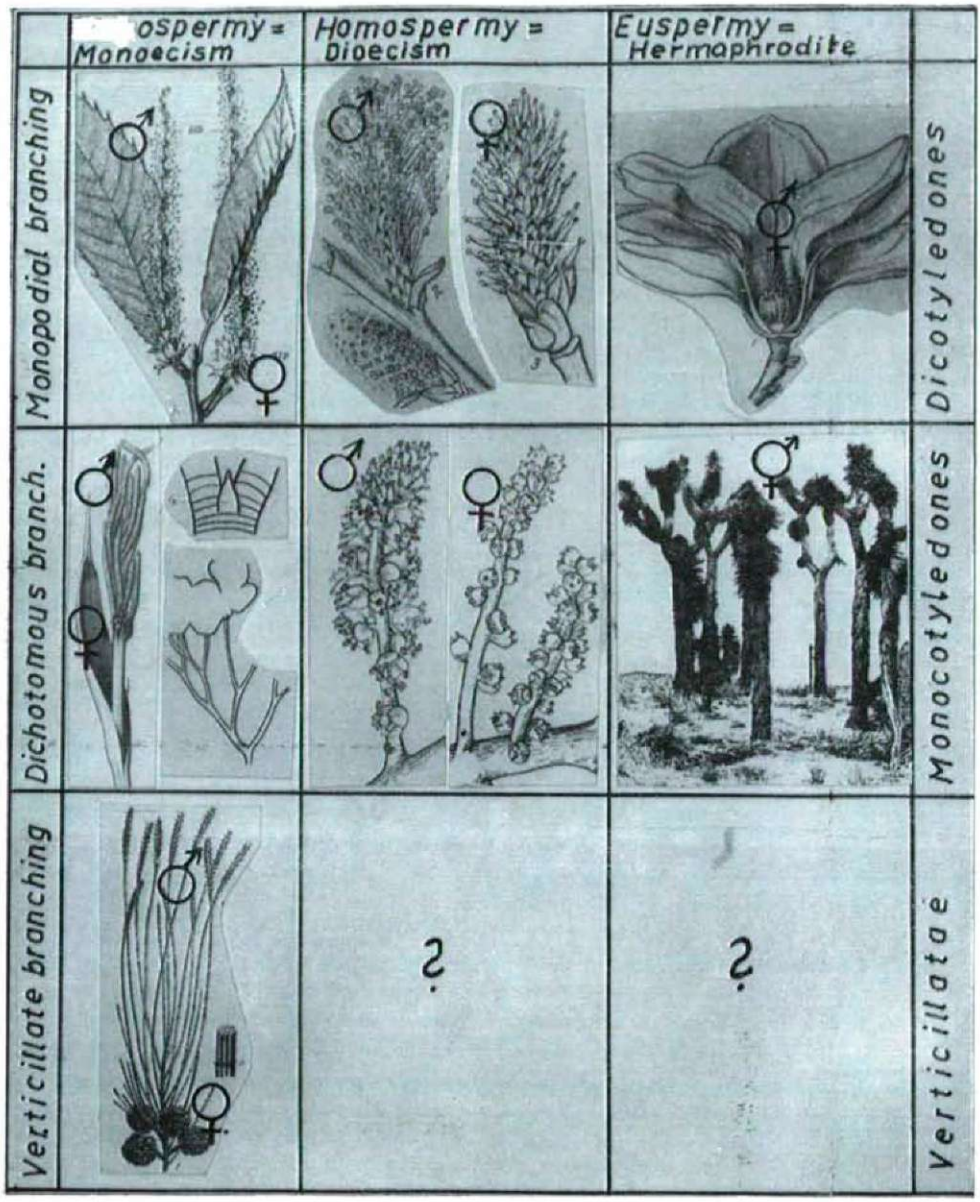


Fig. 27. The dicotyledonous and monoecious *(isosperm) Castanea sativa* of monopodial branching. The flower of dioecious *(homosperm) Salix caprea* and of the *(eusperm) Magnolia acuminata*.
2. The palm of dichotomous branching *(isosperm)*, the dioecious *homosperm* palm with dichotomous branching and the hermaphrodite *Yucca arborescens* of dichotomous branching.
3. The monoecious *(isosperm) Casuarina verticillata* of verticillate branching.
All three series are in the developmental stage of *Angiospermae*, but with three different types of branching.

ditism occur. In our opinion, the monoecism or dioecism of the *Monocotyledones* could not have developed from the monoecious or dioecious stage of *Dicotyledones* neither the hermaphrodite condition of the *Monocotyledones* from the analogous condition in the *Dicotyledones;* these derive, to all probability, from the *Bennettites,* which seems to evidence that the origin of monocotyledons is independent of the origin of dicotyledons. Consequently the *Angiospermae* do not originate from a single common phylum, but at least from two or three phyla substantially differring from each other, and according to the athor's opinion so they are of polyphyletic origin.

Summary

1. Phylogenetic stages. As established in the previous chapters and in accordance with the present state of science, in the history of evolution of the vegetable kingdom the terrestrial plant from their beginnings in the inorganic wordl during their development in the course of 2 to 4 thousand million years passed through the following stages:

Stage I. Beginning of the + and — contrast among the inorganic compounds and their transformation into living compounds.

Stage II. **Virophyta.** Physiological differentiation of the + and — character in the simplest forms of life at the boundary of the inorganic and organic worlds.

Stage III. **Bacteria and Cyanophyceae.** Simplest uni or pluricellular plants without a definite cell nucleus, with + and — sexuality and concealed alternation of generations.

Stage IV. **Monadophyta.** Unicellular plants with definite cell *nucleus,* living both in water and on land, with definite + and — sexuality and alternation of generations.

Stage V. **Algophyta.** Unicellular cell-filamentous, cell-lamellar, cell-bodied plants living both in water and on land, with definite + and — sexuality and alternation of generations, where the gametophyte is multicellular, the sporophyte unicellular or homomorphous with the gametophyte.

Stage VI. **Bryophyta.** Sexually differentiated cormophyt plants, living in water but mainly on land, in which the multicellular gametophyte is physiologically independent and more developed than the equally multicellular sporophyte. The sporophyte has no contact with the soil and is nourished by the gametophyte.

Stage VII. **Psilophyta.** Partly extinct (fossile) terrestrial or aquatic sporipherous plants where the gametophyte and the sporophyte were about equally developed.

Stage VIII. **Pteridophyta.** Terrestrial or aquatic sporipherous plants in which the sporophyte is physiologically independent and much more developed than the physiologically equally independent gametophyte. Both the sporophyte and the gametophyte are in contact with the soil or with the water.

Stage IX. **Pteridospermae.** Extinct (fossile) terrestrial plants which in their exterior are suggestive of the *Pteridophyta*, where the gametophyte of both sexes has developed on the sporophytic mother plant, the female gametophyte had been covered by a thinner or thicker integument and which after fertilization had developed to seed. The medium between the two sexes is probably still the water.

Stage X. **Gymnospermae.** Terrestrial plants in which the enclosed female gametophytes develop as open structures on the strongly developed sporophyte. The unicellular male gametophytes, independently from the liquid water, through the intermediary of the liquid water, through the intermediary of the wind and of the pollen tube get near the female gametophytes while from the seeds originating from the fertilized female gametophytes monoecious and dioecious individuals, sporophytes arise.

Stage XI. **Chlamydospermae.** Spermatophytes in which the female gametophyte is already more cut off from the environment; the male gametophytes come to get near the female gametophyte by the intermediary of the wind, exceptionally of insect or the pollen tube respectively. From the fertilized female gametophyte such seeds develop on the female sporophyte which give rise to dioecious sporophytic individuals only.

Stage XII. **Angiospermae.** Terrestrial spermatophytes in which the female gametophyte is already completely cut off the immediate environment and the fusion with the male gametophyte at fertilization can only take place by the pollen tube. The seeds developing from the fertilized gametophyte give rise to sporophytes with monoecious dioecious or hermaphrodite (monoclinous) flowers.

As demonstrated above, each phylogenetic stage is characterized by properties involving distinct differences from all other developmental stages before or behind it and which differences evolved from each other during many million years from the similar previous forms.

Probably no research worker has or could have any doubt about the natural stages listed, therefore these findings can be taken as basis for further investigation.

2. Sexuality is an objective natural law.

It is an universal law of nature that the individuals of living beings, unicellulars as well as the most developed phanerogams, in their vital processes besides the instinct of self preservation have been and are directed always by the instinct of race preservation, of sexuality, of + and —, male and female character and that the substances carrying the determination of sexuality (gametes) are manifesting themselves most conspicuousli in the sexual organs and in their appearance respectively. Without sexuality and development of sexual organs the gradual evolution of the vegetable kingdom through thousand million years can not be conceived. Sexuality is not an occasional morphological

property but a character phylogenetically fixed in the species, a fundamental principle, a natural law under the cogent influence of which the whole living world stood from the very beginning and still stands in our days.

3. Monoecism and dioecism are objective laws of nature.

With the above fundamental law by necessity an other biological law is linked according to which in the sexual processes the evolution of the species and the formation of new species is furthered in the first place by heterofertilization. This principle materialized in the vegetable kingdom by different means. Its simplest way is seen in the unicellular organism where within the species individuals of opposite sex, monoecious or dioecious come into existence. If on the other hand the individuals are multicellular, the sexual cells of different sex develop either in the various cells or organs of the same individual, when the individuals are essentially again monoecious, or the male and female sexual cells, the gametes, develop in the cells or organs respectively of two different individuals, consequently the members of the species sexually, physiologically and morphologically completely separate from each other, thus the individuals are essentially dioecious.

Monoecism or dioecism are in all phylogenetic stages invariably carried by the sexual cells *(gametes)* or the asexually originated cells *(spores)* or by the *seeds* arising from the sexual process in a way that in each phylogenetic stage monoecism or dioecism according to the environmental conditions always appears. Thus monoecism and dioecism form a basic biological law and their immediate causes can be always traced back to contrasting chemical compounds of to cell particles by which they are carried.

In the course of phylogeny monoecism and dioecism materialized in the various developmental stages as follows.

I. *Virophyta*			
II. *Bacteria*			
III. *Cyanophyta*			
IV. *Monadophyta*	*Monoecism*	*Dioecism*	*Dioecism*
(Flagellatae)	Isogamy	Homogamy	Anisogamy
V. *Algophyta*			
(Chlorophyta)	Isozygote	Homozygote	Heteromorphism
(multicellular)			
VI. *Bryophyta*	Isospore	Homospore	Anisozygote
and *Charophyta*			?
VII. *Psilophyta*	Isospore (?)	Homospore (?)	Anisospore?
VIII. *Pteridophyta*	Isospore	Homospore	Heterospore
IX. *Pteridospermae*	Isospermy	Homospermy	(Heterospermy?)
X. *Gymnospermae*	Isospermy	Homospermy	(Euspermy?)
XI. *Chlamydospermae*	—	Homospermy	(Euspermy?)
XII. *Angiospermae*	Isospermy	Homospermy	Euspermy

Accordingly in the various developmental stages monoecism and dioecism from the condition of the unicellular gametes to the Angiosperms always existed and continue to exist in our days.

4. The branching of monoecious and dioecious plants.

Both monoecism and dioecism appear in the various developmental stages never in a single form but invariably in 2 or 3 basic forms of branching. The unicellular organisms exhibited an incredible variety of forms; the main types of branching began to develop from them.

The main types of the branching in multicellular organisms can be traced back in the final result to 3 basic types, the monopodial, dichotomous and verticillate types. These 3 main types of branching were from the multicellular stage of *Algae* to the stage of Angiosperms in all periods closely connected with sexuality and although they underwent some modification in the course of phylogeny still they maintained the ancient character of branching even on the most developed forms until the present day.

Within the individual developmental stages and systematic groups there are so deep differences in branching that it is almost impossible to assume that they might have originated from each other, e. g. *Musci* and *Hepaticae* within the Mosses, and *Lycopsida, Pteropsida* and *Sphenopsida* within the *Pteridophita.*

5. The joint appearance of (1) sexuality, (2) monoecism-dioecism and (3) branching in the various phylogenetic stages.

In the Table which follows, the 3 main forms of sexuality; monoecism, homomorphous and heteromorphus dioecism are established and brought into connection with the systematic categories prevailing in our days and with the three main forms of branching.

If from this survey it can be established that in the course of evolution the individual phylogenetic stages always appeared in the three main types of branching and in the condition of monoecism or dioecism *(isogamy, homogamy, anisogamy, isospore, homospore, anisospore, isosporophyllum, homosporophyllum, heterosporophyllum, isospermy, homospermy* and *euspermy)* so it can be surmised and properly so, that the individual phylogenetic stages in the course of the history of evolution continued or have been modified always in the same type of branching from which they themselves derived. Since these main types of branching, i. e. the monopodial, dichotomous and verticillate types of branching existed from the algal stage to the Angiosperms, and continued to exist to our days, so the assumption is justified that the higher forms of monopodial branching derived from the less developed but also monopodial stages and not from the dichotomous or verticillate. This assumption is also inversely valid, namely these main types of branching did not originate anew in each higher developmental stage and in each subsequent geological period. E. g. all three forms of branching of the Psilophytes of the Devonian or all three forms of branching of the Pteriodophytes of the Carboniferous, or all three types of branching of the Gymnosperms or Angiosperms of the Permian brought both their monoecious and dioecious conditions and types of branching with them from the previous periods, for instance the *Monocotyledones* the dichotomous and the *Dicotyledones* the monopodial branching.

It should be noted by the way that there is no perfectly dichotomously branching dicotyledonous lignous plant nor ever has been; such can occur

only among the Monocotyledons (*Palmae, Yucca, Dracaena* etc.). — Consequently the development must have been from the very beginning and by necessity polyphyletic, because it can be explained only by such polyphyletic development that in the existing systems at the same developmental stage forms of widely different branching could get beside each other the derivation of which from each other is not possible with any effort.

The individual evolutionary phases (I—XII) and within these the types of branching and the distribution of the sexual organs are included in the following combined table in which the author intends to present the evolutional system of the fresh water and terrestrian plants independently of the sea plants. In a separate global table the author presents his triphyletic evolutionary system including the characteristic representants of both fossil and recent fresh-water and terrestrial vegetation according to evolutionary degrees and geological ages. The distribution of the system is as follows.

SUMMARY

Stage I. Inorganic and organic substances + and — compounds.

Stage II. *Virophyta*

+ and — compounds, two opposite effects of DNA.

Stage III. *Bacteria* **and** *Cyanophyceae.*

1. Isogamy (monoecism)?
2. Homogamy (dioecism)?

Stage IV. *Monadophyta (Flagellatae)*

1. Isogamy (monoecism)	*Protococcales*	*Heterocontae*	*Volvocales*
2. Homogamy (dioecism)	*Desmidiaceae* *Diatomeae*	*Volvocales*	*Chrysophyceae*
3. Anisogamy (dioecism)		*Volvocales*	

Stage V. *Algophyta (Chlorophyta)*

	Cell filament	**Monopodial**	**Dichotomous branching**	**Verticillate**
1. Isozygota (g. monoecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*	*Syphonales*	*Ulotrichales*
2. Homozygota (g. dioecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*	*Syphonales*	*Ulotrichales*
3. Anisozygota (g. dioecism)	*Oedogoniales* *Ulotrichales* *Conjugatae*	*Ulotrichales* *Siphonocladales*		
4. Homomorphous (dioecism)	*Siphonocladales*	*Syphonales*	?	*Ulotrichales*

Stage VI. *Bryophyta* **and** *Charophyta*			
1. Isospore (g. monoecism)	*Musci*	*Hepaticae*	*Charales*
2. Homospore (g. dioecism)	*Musci*	*Hepaticae*	*Charales*
3. Anisospore (dioecism)	*Musci*	*Hepaticae*	*Charales*
Stage VII. *Psilophyta*			
1. Isospore (g. and sp. monoecism)	*Hornea* *Rhynia*	*Protopteridium* *Psilotum*	*Calamophyton*
2. Homospore (g. dioecism sp. dioecism)	?	?	?
3. Anisospore (g. dioecism sp. monoecism)	?	?	?
Stage VIII. *Pteridophyta*			
1. Isosporophyllum (g. and sp. monoecism)	*Lycopodinae*	*Filicinae*	*Equisetinae* *Sphenophyllum*
2. Homosporophyllum (g. dioecism, sp. monoecism)	*Lycopodinae*	*Parkeriaceae*	*Equisetinae*
3. Heterosporophyllum (g. dioecism, sp. monoecism)	*Lepidodendron* *Selaginellales*	*Sigillaria* *Hydropterides* *Isoëtes* *Stylites*	*Calamites*
Stage IX. *Pteridospermae*			
1. Isospermy (g. dioecism, sp. monoecism)	*Lepidocarpon*	*Lyginodendron*	*Calamocarpon*
2. Homospermy		?	?
Stage X. *Gymnospermae*			
1. Isospermy (g. dioecism, sp. monoecism)	*Pinaceae* *Taxodiaceae*	?	*Cupressaceae*
2. Homospermy (g. and sp dioecism)	—	*Araucariaceae* *Cordaites(?)* *Ginkgoaceae* *Cycadales* *Podocarpaceae* *Taxales*	*Cupressaceae*
3. Euspermy (hermaphrodite?)	*(Coniferae?)*	*Bennettites*	—
Stage XI. *Chlamydospermae*			
1. Isospermy (monoecism)	—	—	?
2. Homospermy (g. and sp. dioecism)	*Gnetum*	*Welwitschia*	*Ephedra*
Stage XII. *Angiospermae*			
1. Isospermy (g. dioecism sp. monoecism)	*Monochlamydeae*	*Cyperales* *Palmae*	*Verticillatae*
2. Homospermy (g. and sp. dioecism)	*Monochlamydeae*	*Palmae*	—
3. Euspermy (hermaphrodite) (g. and sp. monoecism)	*Dialipetalae*	*Liliflorae*	*(Sympetalae??)*

Natural system of the Landsplants (after the author)

I. Stage **Virophyta**

II. Stage **Anucleophyta**

III. Stage **Monadophyta**

IV. Stage **Algophyta**

(Mykophyta)

1. *Chlorophyta* *(Lichenes)*	2. *Chlorophyta* *(Phaeophyta [?])*	3. *Chlorophyta* *(Rhodophyta(?))*

V. Stage **Bryophyta** et **Charophyta**

1. *Musci*	2. *Hepaticae*	3. *Characeae*

VI. Stage **Psilophyta**

1. *Prolycopsida*	2. *Propteropsida*	3. *Prosphenopsida*

VII. Stage **Pteridophyta**

1. *Lycopsida*	2. *Pteropsida*	3. *Sphaenopsida*

VIII. Stage **Pteridospermae**

1. *Lepidospermae*	2. *Pterispermae*	3. *Calamospermae*

IX. Stage **Gymnospermae**

1. *Isospermae* *(Coniferales)*	2. *Homospermae* *(Cycadales)*	3. *Cupressospermae* *(Cupressales)*

X. Stage **Chlamydospermae**

1. *Gnetales*	2. *Welwitschiales*	3. *Ephedrales*

XI. Stage **Angiospermae**

1. *Dicotyledones*	2. *Monocotyledones*	3. *Verticillatae*

*

This survey is intended as the expression of a concept concerning the polyphyletic evolution of the vegetable kingdom, the probability of which — as demonstrated by the foregoing — is supported by a number of positive facts and natural laws.

The principles of the above concept were laid down by the author as a young botanist 47 years ago in his paper "*Ein Gedanke zur polyphyletischen Entwicklung der Pflanzenwelt*" (Beihefte zum Bot. Centralblatt, 1918.) and expounded in the present paper probably for the last time. Supported by new scientific arguments the discourse might contribute to the elucidation of an extremely important and interesting problem.

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SPOROPHYTA

SPERMATOPHYTA

RAMIF	ALGOPHYTA	BRYOPHYTA	PSILOPHYTA	PTERIDOPHYTA		PTERIDOSPERMAE	GYMNOSPERMAE		CHLAMYDOSP.	ANGIOSPERMAE
		Iso-homosporia	Iso-homosporia	Iso-	homo- heterosporia	Iso-homospermia	Isospermia(Monoecia)	Homospermia (Dioecia)	Homospermia (Dioecia)	Iso-homo- euspermia
	Palaeophyticum						Mesophyticum		Kainophyticum	

MONOP. — MONOPHYTA

DICHOT. — DICHOTOPHYTA

VERTICILL. — VERTICILLATOPHYTA

Chlorophyceae
Pleurocarpi
Musci
Acrocarpi
Eriopus
Nostra
Rhynia
Psilodendrion
Hornea
Lycopodium
Drepanophycus
Protolepidodendron
Selaginella
Lepidostrobus
Cyclostigma
Lepidodendron
Pinaceae
Lepidocarpon
Geinitzia
Taxodiaceae
Sphenolepidium
Voltzia
Dialipetalae
Degeneria
Gnetum
Monochlamydeae
Chlorophyceae
Hepaticae
Asteroxylon
Psilotum
Tmesipteris
Filicinae
Eusporangiatae
Filicinae
Leptosporangiatae
Parkeriaceae
Hydropterides
Isoëtales
Sigillaria
Pleuromeia
Physostoma
Cladoxylon
Hepaticites
Zosterophyllum
Aneurophyton
Megaphyton
Coenopteridales
Asterotheca
Callixylon
Foerstia
Taeniocrada
Pseudosporochnus
Protopteridium
Medullosae
Lyginodendron
Odontopteris
Lebachia
Neuropteris
Palaeotaxus
Archeopodocarpus
Cordaites
Cycadinae
Taxales
Williamsonia (Bennettites)
Podocarpaceae
Ginkgo
Baiera
Cayoniales
Cycadeoidea (Bennettites)
Araucariaceae
Welwitschia
Palmae
Liliiflorae
Cyperales
Yuccites
Chlorophyceae
Characeae
Equisetaceae
Protocalamites
Calamophyton
Hyenia
Asterocalamites
Pseudobornia
Sphenophyllum
Calamites
Equisetites
Neocalamites
Cheirostrobus
Calamostachys
Schizoneura
Phyllotheca
Calamitocarpon
(Chamaecyparis)
Cupressaceae
(Callitris)
Ephedraceae
Casuarinaceae

Rajzolta: DÖRFLINGER E.

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